# Does disturbance favour weak competitors? Mechanisms of changing plant abundance after flooding

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#### Abstract.

**Question:** Does disturbance reduce competition intensity and thus favour weak competitors that are presumably less affected by disturbance than strong competitors?

**Methods:** We used a single flooding event with increasing duration to simulate disturbance with increasing intensity. Six flood-plain grass species, typical of different flood regimes were grown in monocultures and in an additive species mixture. Flooding took place early in the first growing season and changes were monitored until the end of the second growing season.

**Results:** Longer flooding durations initially decreased competition, but only a single species (*Agrostis*) increased its abundance in mixtures after flooding. The two weakest competitors in our selection (*Poa trivialis* and *Elytrigia repens*) failed to benefit from flooding because direct losses from flooding exceeded gains from reduced competition. Accordingly, we found no trade-off between flooding tolerance and competitive ability indicating that floods affect strong and weak competitors equally, although some species tolerated floods better than others.

**Conclusions:** Since competition is only temporarily weakened after disturbance, increased competitive ability relative to other species may provide a more effective strategy for persistence in flood-disturbed sites. Above-ground runners seem an important prerequisite for enhanced competitive ability of clonal species in flood-disturbed sites.

**Keywords**: Clonal growth; Competitive ability-tolerance tradeoff; Competitive hierarchy; Competitive release; Flood tolerance; Trade-off; Zonation.

Nomenclature: van der Meijden (1996).

**Abbreviations:**  $\ln RR = \text{natural log of the response ratio; <math>LT_{50} = \text{number of days}$  ('lethal time') after which 50% of individuals had died.

## Introduction

There is general agreement that disturbance, environmental factors causing loss of plant parts or densityindependent mortality (*sensu* Grime 1979; Tilman 1988), play a major role in determining species distribution. Species ranges usually have a clear limit at both extremes of spatial and temporal disturbance gradients. These limited species distributions have been demonstrated for a wide variety of disturbance agents, including flooding (Keddy 1984; Pollock et al. 1998), wave exposure (Shipley et al. 1991), fire (Collins et al. 1995; Jutila & Grace 2002; Laterra et al. 2003) and drought (Silvertown et al. 1999).

Disturbance-induced competitive release has often been proposed as a mechanism underlying these distribution patterns (Grime 1979; Huston 1979). This hypothesis states that intense competition at the least disturbed parts of disturbance gradients excludes species with low competitive ability, here defined as the ability to resist suppression by other species - i.e. 'competitive response' sensu Goldberg (1996). Because the weaker competitors are more tolerant to disturbance, they find a refugium at the most disturbed end of the gradient. The hypothesis first predicts that disturbance decreases the intensity of competition and thus allows weak competitors to increase in abundance relative to non-disturbed environments (Grime 1979; Huston 1979; Keddy 1990). A second prediction is a trade-off between a species ability to tolerate disturbance and the ability to resist suppression by other species (Huston 1979; Petraitis et al. 1989).

An alternative explanation for increased abundance after disturbance is provided by the hypothesis of 'competitive change' (*sensu* Suding & Goldberg 2001). It predicts that certain species increase in competitive ability relative to other species (Tilman 1988; Taylor et al. 1990), whereas competitive release predicts a consistent hierarchy of competitive abilities (Goldberg 1996). Competitive change seems possible because species differ in tolerance to disturbance. Disturbance may thus change size distribution and relative abundance and thereby affect a species competitive ability (Schmid & Harper 1985; Wedin & Tilman 1993; Vilà & Terradas 1995; Suding & Goldberg 2001). Increased competitive ability relative to other species may reflect long-term persistence (Crawley 1990) without the need of subsequent disturbance, whereas in case of competitive release, weak competitors strongly depend on regular disturbance to persist (Huston 1979). In this paper we report on an experiment that purports to test the competitive release relative to the competitive change hypothesis.

Experimental evidence for competitive release produced thus far suffers from three major shortcomings. First, validity of competitive release has rarely been tested for species that rely on clonal persistence during disturbance, although this is an important strategy in relation to disturbance (McIntyre et al. 1995; Pausas & Lavorel 2003). Secondly, most studies have only tested whether disturbance weakens competition (Wilson & Shay 1990; Campbell & Grime 1992; Wilson & Tilman 1993, 1995; Turkington et al. 1993), whereas actual benefits from disturbance also require that gains from decreased competition outweigh losses from disturbance (Chesson & Huntly 1997). Explicit tests for benefits have either been ignored (e.g. Wilson & Shay 1990; Campbell & Grime 1992; Turkington et al. 1993, but see Vilà & Terradas 1995) or effects of competition were measured on target plants that were not affected by disturbance (e.g. Wilson & Tilman 1993, 1995). Thirdly, we are not aware of studies that tested for a trade-off between disturbance tolerance and competitive ability. Although competitive abilities have been related to positions on wave exposure (Wilson & Keddy 1986) and salt marsh flooding gradients (e.g. Bertness 1991; Pennings & Callaway 1992), these gradients also constitute variation in salinity and/or nutrient availability (Wilson & Keddy 1986; Bockelmann & Neuhaus 1999; Emery et al. 2001).

Here, we measured effects of competition and flooding on six clonal grass species. Our flooding treatment consisted of different durations of a single flooding event to simulate disturbance regime of flood-plains in downstream parts of rivers in the temperate climatic zone (Pollock et al. 1998; Vervuren et al. 2003). We tested the following hypotheses based on the predictions of competitive release: 1. Weak competitors benefit from flooding, i.e. increase in abundance in flooded relative to non-flooded mixtures. 2. These benefits are due to a decrease in competition intensity, instead of an increased competitive ability relative to other species. Flooding will therefore, at least temporarily, decrease competition intensity but not affect the species hierarchy of competitive abilities. 3. There is an inverse relationship between flooding tolerance and competitive ability.

## **Material and Methods**

#### Species selection

We selected six grass species which are all characteristic of productive hay fields in flood-plains of the lower River Rhine. Here, *Arrhenatherum elatius* and *Lolium perenne* dominate the highest elevation, *Alopecurus pratensis* and *Poa trivialis* intermediate positions whereas *Elytrigia repens* and *Agrostis stolonifera* dominate the most frequently flooded parts of floodplain grasslands (Sýkora et al. 1988; Blom & Voesenek 1996). For brevity, species will hereafter be referred to by their generic name.

For all six species, abundance after disturbance strongly depends on survival and resprouting capacity (Lavorel et al. 1997), either because vegetative tillering is the main mode of lateral dispersal, in case of *Agrostis*, *Elytrigia* and *Poa*, or because their seeds lack dormancy or traits for long-distance dispersal, in case of *Alopecurus*, *Arrhenatherum* and *Lolium* (Bullock et al. 1995; Thompson et al. 1997).

## Experimental procedure

The experiment was set up as a randomized block design with five blocks that each contained one replicate of each monoculture (six in total) and species mixture (containing all six species) for each of six flooding treatments, i.e. 0, 10, 20, 30, 40 and 50 days of submergence during the first growing season. These treatment levels covered the entire range of flooding durations that may occur during the growing season in grasslands along the River Rhine (Vervuren et al. 2003).

The competition treatment followed an additive design where the density of each species was similar in monocultures and mixtures. As a consequence, the total initial density in mixtures was six times higher than in monocultures (Gibson et al. 1999). Although precluding quantitative predictions on population dynamics (Inouye 2001) this design provides a firm basis for ranking responses to interspecific competition across a range of species and environments (Gibson et al. 1999; Inouye 2001).

Vegetative material of all species was collected in flood-plain grasslands of the River Waal, the main branch of the River Rhine in the Netherlands, between 22 and 26 March 1999; each species was collected from a single population but a minimum distance of five meter was kept between sampled plants to guarantee genetic variation. From the collected tussocks and stolons, a maximum of four, single tillers (with roots) were isolated and planted in separate pots (6 cm diameter) in a sand/clay mixture (1:1; v/v) and left to grow in a greenhouse with a minimum day length of 16 h and a minimum temperature of 10 °C.

Plastic containers (length × width × depth =  $39.5 \times 29.5 \times 19.8$  cm) were filled with 20 L of a sand/clay mixture (1:1; v/v) after mixing the soil with 55 g osmocote slow release (9 months) fertilizer. Each container thus received 8.25 g N, 6.05 g P, 7.15 g K and 1.1 g Mg. On 30 May 2000 each container was supplied with additional nutrients in the form of osmocote slow release (3 - 4 months) grains containing a total of 3 g N, 2.2 g P, 2.6 g K and 0.4 g Mg, so that each experimental unit received, for the remaining period of the experiment, about the same amount of nutrients as the previous year. The bottom of each container contained holes and a 0.5 cm layer of gravel to improve drainage. A polyethylene sheet was placed on top of the gravel to isolate roots from the gravel.

Between 12 and 16 April 1999 tillers were transplanted to the monocultures and species mixture. Tillers from the same tussock or stolon were planted in different containers. Each container was used for either a single monoculture or a species mixture. In each monoculture 15 tillers were planted at random positions. In the species mixture a total of 90 tillers, i.e. 15 for each species, were planted in random positions, but at regular distances between each shoot. After transplanting, containers were left in the greenhouse for another three weeks and thereafter placed outdoors for acclimatization. All containers assigned to flooding treatments were submerged at 10 May 1999 in five outdoor ponds  $(\text{length} \times \text{width} \times \text{depth} = 1000 \times 180 \times 90 \text{ cm};)$ . Water levels were raised to 50 cm above the top of the containers to realize complete submergence. After 10, 20, 30, 40 and 50 days one replicate of each monoculture and the species mixture was taken out of each of the five ponds and placed outdoors under drained conditions in the University garden. Here, the area was subdivided into five separate blocks and all containers from the same pond were placed in the same block. Each 'garden block' also contained one replicate of each monoculture and the species mixtures that were left unflooded, i.e. the control treatments. Each block thus contained 42 containers, six flooding treatments × seven species combinations (six monocultures and one mixture), and the total experiment 210 containers.

Soon after placing the containers under drained conditions they were surrounded by white polystyrene boards, up to 20 cm above the top of the containers, to prevent interference with plants in neighbouring containers. In dry periods containers were regularly watered with tap water.

## Plant measurements

We measured abundance three days after the end of submergence and simultaneously counted the individuals that had survived in monocultures. Abundance in nonflooded containers was measured simultaneously with the containers that had been submerged for 10 days. Subsequent measurements of abundance were taken in August 1999 and at the end of the experiment, September 2000.

Abundance was determined with the point quadrat method that allowed repeated non-destructive measurements. A point quadrat frame was built that fitted the experimental containers. A perspex sheet with holes was placed ca. 50 cm above the soil surface and attached to the containers by four threaded steel legs fixed in the margin of the containers and in an iron frame around the bottom of the containers. The grid consisted of 40 5-mm holes placed in eight columns and five rows with a distance of 40 mm between holes; there were no recordings within 25 mm of the rim of the container. To guarantee a vertical position of pins a 15-mm high rubber tube was placed above each hole on top of the sheet. All touches on a pin were recorded.

Point quadrat scores provided a stand-level parameter, i.e. total abundance per experimental unit, but the use of perennial grasses, and some with vigorous lateral spread, already precluded identification of individuals. Point quadrat measurements have been shown to provide good estimates of (temporal changes in) cover of grassland species (Mitchley & Grubb 1986; Stampfli 1991) and may also reflect above-ground dry weight. Linear regression of (In-transformed) point quadrat scores against above-ground dry weight of monocultures gave a significant relationship for most species: Agrostis ( $R^2 = 0.41$ ; n = 29; P = 0.001); Alopecurus ( $R^2 = 0.29$ ; n = 27; P = 0.005); Arrhenatherum ( $R^2 = 0.00$ ; n = 15; P = 0.93); *Elytrigia* ( $R^2 = 0.47$ ; n = 30; P < 0.001); *Lolium* ( $R^2 = 0.75$ ; n = 15; P < 0.001); *Poa* ( $R^2 = 0.73$ ; n = 15; P < 0.001).

#### Response parameters

To test the second and third hypothesis we calculated the response ratio (Hedges et al. 1999):

$$\ln RR_{f} = \ln \left( Y - mix_{f} / Y - mono_{f} \right)$$
(1)

InRR denotes (the natural logarithm of) the response ratio, Y-mix refers to the abundance in the species mixture, Y-mono to the abundance in monocultures and the subscript f denotes the flooding treatment, i.e. 0, 10, 20, 30, 40 or 50 days. Within a species-across-treatment levels, lnRR-values indicate changes in competition intensity since weaker competition after flooding disturbance corresponds with larger (less negative) lnRR values. When compared among species, lnRR provides a measure of relative competitive ability because stronger competitors will have higher response ratios than weaker competitors.

To assess flooding tolerance of each species we fitted survival as a function of flooding duration with a logistic function to estimate  $LT_{50}$ , the number of days after which 50% of the individuals in monocultures had died (Vervuren et al. 2003). As a second measure of flooding tolerance we determined the decay rate as the slope in linear regression of ln-transformed values of abundance (measured in monocultures immediately after flooding) against flooding duration. Values of non-flooded monocultures were excluded to avoid spurious correlation with lnRR<sub>0</sub> values when testing for a trade-off (see next section).

#### Data analysis

For each species separately, we tested the effect of block, flooding duration and competition treatment with ANOVA (Norusis 1999) using abundance at the end of the first and second growing season as a withinrepeated factor. In the analyses of abundance, we only included controls (non-flooded) and those flooding durations with survival in at least three replicates per competition treatment, as a consequence degrees of freedom for flooding treatment differed between species. Prior to analysis, all data were In-transformed to achieve homogeneity of variances and normal distribution of residuals (Sokal & Rohlf 1995). To test whether abundance in flooded mixtures had changed relative to non-flooded mixtures, as stated in our first hypothesis, we compared abundance in each flooded mixture with the non-flooded mixture using least significant difference and Dunn-Sidák adjusted significance levels (Sokal & Rohlf 1995). Weaker competition due to flooding would surface both as a significant flooding × competition term in the ANOVA on abundance values and as less negative values for lnRR. To test for a shift in species competitive hierarchy we ran another ANOVA with block, species and flooding as independent variables and lnRR values in the first and second year as a within-repeated factor. Significant species × flooding terms were considered contradictory to our second hypothesis that predicted a consistent competitive hierarchy.

Our third hypothesis, predicting a negative relationship between competitive response (lnRR) and flooding tolerance (LT<sub>50</sub> and decay rate), was tested with Pearson *r*-correlation on species means. We restricted the analysis to lnRR<sub>0</sub> values of the second growing season because competitive abilities as determined after a single growing season may be unrealistic by not accounting for seasonal effects (Wedin & Tilman 1993; Gibson et al. 1999). Next we determined how many species were required for a sufficiently powerful distinction between the null hypothesis (no relationship) and the alternative hypothesis (an inverse relationship). The correlation coefficient according to the alternative hypothesis was calculated under the assumption that a trade-off between flooding tolerance and competitive ability would have been found if the species with the highest lnRR<sub>0</sub>-value had the lowest tolerance to flooding and the most tolerant species had the lowest lnRR<sub>0</sub>-value (sensu Fernández & Reynolds 2000). The slope connecting these points was calculated and converted to a correlation coefficient by multiplying the slope with the ratio of standard deviations for flooding tolerance and competitive ability (Cohen 1988 p. 77). Using this correlation coefficient as the alternative hypothesis, we consulted tables in Cohen (1988) to determine how many species would have been required to reject the null hypothesis with a probability of 80% ( $\beta = 0.80$ ). Because the sign of the correlation coefficient was an explicit part of the hypothesis, we used the one-tailed test at  $\alpha = 0.05$ .

#### Results

## Effects of flooding on abundance

Species survival after flooding corresponded well with their position along the flooding gradient. Flooding durations of 30 days and longer killed all of the high-elevated species *Arrhenatherum* and *Lolium*. Intermediate *Poa* did not survive the longest flooding treatment, whereas the other intermediate species *Alopecurus* disappeared in some replicates of this flooding duration. The lower elevated species *Agrostis* and *Elytrigia* survived 50 days of flooding in all containers.

For Arrhenatherum, Alopecurus, Agrostis and Elytrigia effects of flooding on abundance varied significantly between both years (Table 1), reflecting the gradual recovery from flooding (Fig. 1). At the end of the second growing season, all surviving plants of these four species appeared to have recovered completely, because abundance in flooded monocultures was equal to the non-flooded monoculture at that time (Fig. 1). Lolium and Poa will have recovered faster since their abundance after flooding was already similar to non-flooded monocultures at the end of the first growing season (Fig. 1), although abundance of these two species immediately after flooding was also strongly reduced (data not shown).

In species mixtures, flooding significantly increased abundance of *Agrostis* and significantly decreased abundance of *Arrhenatherum* and *Alopecurus* compared to non-flooded mixtures (see asterisks in Fig. 1). For all species, these effects of flooding appeared to be persistent since they were still noticed at the end of the second growing season (Fig. 1).

## Competition after flooding

Whether flooding changed the effect of competition on a particular species is indicated by significant interactions between flooding and competition on abundance (Table 1). The direction and magnitude of these changes are most clearly illustrated by comparing lnRR values of a species across flooding durations (Fig. 2). As shown by significant competition  $\times$  flooding and year  $\times$  competition  $\times$  flooding terms (Table 1), flooding had influenced competitive responses for *Alopecurus, Agrostis* and *Elytrigia* while a marginally significant effect of flooding was noted for *Poa* (Table 1).

Especially in the first year, flooding appeared to weaken competition because response ratios significantly increased with flooding duration for all four species that survived more than 20 days of flooding (Fig. 2). In the second year however, effects of flooding on competition appeared species-specific. Competitive responses for *Poa* had returned to the nonflooded level. For *Elytrigia*, comparison of lnRR between flooding treatments with non-orthogonal contrasts revealed no difference between non-flooded and flooded treatments, but only between short and long flooded treatments (results not shown). *Agrostis* still experienced weaker competition in flooded mixtures during the second year. For *Alopecurus* however competition appeared to be stronger after 40 days of flooding relative to non-flooded conditions. This was indicated by a significant non-orthogonal contrast ( $F_{1,36} = 30.71, p < 0.001$ ) of 0 days versus 40 days of flooding within the competition × flooding term in ANOVA on abundance (Table 1), combined with the more negative lnRR after 40 days of flooding (Fig. 2).

## Effect of flooding on competitive hierarchy

As shown by the significant main effect of species for response ratios (Table 2) competitive responses significantly differed between species, demonstrating a competitive hierarchy in our group of species. However, when flooding durations of 30 and 40 days were included in the analysis this hierarchy was also significantly affected by flooding (significant species  $\times$  flooding term in Table 2). This shift mainly appeared to result from the increased competitive ability of *Agrostis* relative to *Alopecurus* after long flooding (Fig. 2).

## Competitive ability – flood tolerance trade-off

In contrast to our third hypothesis, neither  $LT_{50}$  nor decay rate was negatively related to competitive response (Fig. 3). If the strongest competitor would have been the least tolerant species and if the most tolerant species would have been the worst competitor, the correlation coefficients would have been – 0.95 for  $LT_{50}$  versus competitive ability and – 0.92 for decay

**Table 1.** *F*-values for effects of block, competition, flooding duration and year of measurement on ln-transformed values of abundance of six grass species, dominant in river flood-plain grasslands at high, medium and low elevated positions respectively. Data were analysed with type I Sums of squares using abundance at the end of the first and second year ('Year') as a within-repeated measurement.

	Arrhenatherum		Lolium		Alopecurus		Poa		Agrostis		Elytrigia	
	df	F	df	F	df	F	df	F	df	F	df	F
Block	4	$2.67^{+}$	4	2.07	4	2.99*	1	$2.22^{\dagger}$	4	4.70**	4	4.79**
Competition	1	320.46***	1	169.40***	1	391.90***	1	436.85***	1	273.41***	1	484.80***
Flooding	2	24.95***	2	0.51	4	24.18***	4	1.30	5	4.94**	5	0.59
C*F	2	1.19	2	0.36	4	0.36	4	0.96	5	17.05***	5	3.60**
Error(=MS)	19	0.29	20	0.33	36	0.17	33	0.40	42	0.20	44	0.32
Year	1	37.79***	1	93.63***	1	4.98*	1	164.13***	1	32.57***	1	196.09***
Year*Block	4	0.85	4	1.74	4	2.53†	4	6.42**	1	35.56***	4	2.81*
Year*Competition	1	3.59†	1	69.61***	1	3.29	1	260.43***	1	8.52**	1	50.09***
Year*Flooding	2	8.57**	2	0.07	4	5.64**	4	1.35	5	14.71***	5	3.89**
Year*C*F	2	0.32	2	0.60	4	4.22**	4	$2.42^{\dagger}$	5	$2.41^{+}$	5	1.33
Error(=MS)	19	0.19	20	0.15	36	0.15	33	0.21	42	0.18	44	0.16

Notes: Due to total extinction after certain flooding durations degrees of freedom differ between species. Significance levels:  $^{\dagger} = P < 0.10$  (marginally significant)\* = P < 0.05; \*\* = P < 0.01; \*\*\* = < P 0.001.



**Fig. 1.** Above-ground abundance (means  $\pm$  SE; *n* = 5), measured as point quadrat scores, of each tested species in monocultures (dashed line, open symbols) and species mixtures (solid line, closed symbol) after different periods of total submergence. For clarity, abundance immediately after flooding has been omitted. Panels indicate abundance at the end of the first ( $\triangle$ ) and second growing season ( $\square$ ). Asterisks denote significant differences of indicated flooded mixtures with non-flooded mixtures.

rate versus competitive ability. With such coefficients to be demonstrated as alternative hypotheses, five species are sufficient to correctly reject the null hypothesis (predicting no relationship) with a probability of

80%. Hence, it is not likely that the lack of a trade-off in this study with six species was caused by insufficient statistical power.

**Table 2.** *F*-values for effects of block, species, flooding duration and year of measurement on competitive response (ln RR) in August 1999 and September 2000 (treated as a within-repeated measurement). Data were analysed with type I Sums of Squares using ln RR at the end of the first and second year ('Year') as a within repeated measurement. Due to complete mortality of *Arrhenatherum* and *Lolium* after 30 days of flooding, only controls and 10 and 20 days of flooding were included in analysis 1. Analysis 2 includes controls and 10, 20, 30 and 40 days of flooding. *Arrhenatherum* and *Lolium* were excluded from this analysis.

	An	alvsis 1	Ar	nalysis 2
	df	F	df	F
Block	4	0.27	4	0.84
Species	5	11.71***	3	25.13***
Flooding	2	0.54	4	9.74***
Species × Flooding	10	1.04	12	2.61**
residual (=MS)	66	0.62	73	0.57
Year	1	70.59***	1	205.55***
Year × Block	4	$2.11^{+}$	4	3.27*
Year × Species	5	29.58***	3	77.62***
Year × Flooding	2	1.79	4	6.98**
Year × Species × Flooding	10	1.50	12	0.97
Residual(=MS)	66	0.37	73	0.30

Notes:<sup>1</sup> df = degrees of freedom (effect, error). Both species and block were treated as random factors, and as a consequence flooding was tested against species\*flooding, all other effects against the residual. Significance levels:  $^{\dagger} = P < 0.10$  (marginally significant); \* = P < 0.05; \*\* = P < 0.01; \*\*\* = < P 0.001.



**Fig. 2.** Competitive response (ln (RR<sub>f</sub>), means  $\pm$  SE, n = 5) of tested species after different periods of total submergence in the first growing season. Ln RR was determined at the end of the first ('Year 1') and second growing season ('Year 2'). Abbreviations of species names: Ar = *Arrhenatherum*; Lo = *Lolium*, Al = *Alopecurus*; Po = *Poa*; Ag = *Agrostis*; El = *Elytrigia*.

## Discussion

Our study confirmed that interactions between flooding and competition may result in changed abundance, but our data were inconsistent with competitive release as the underlying mechanism. In contrast to our first hypothesis we found no benefits for the weakest competitors in our selection, i.e. *Elytrigia* and *Poa*. In line with our second hypothesis flooding had reduced competition, but it produced no net increase in abundance of *Elytrigia* and *Poa* in flooded mixtures. This indicates that losses from flooding exceeded gains from reduced competition and underlines the importance of explicitly distinguishing between reduced competition and benefits from disturbance, at least if plants are also directly affected by the disturbance. Finally, there was no evidence for a trade-off between flooding tolerance and



**Fig. 3.** Correlation between species competitive response in non-flooded species mixtures (ln RR<sub>0</sub>) in the second year of the experiment and flooding tolerance, expressed as survival (LT<sub>50</sub>) and decay rate of above-ground abundance as determined immediately after flooding. Symbols indicate species means  $\pm$  SE (n = 5). Pearson correlation coefficient ( $r_s$ ) is indicated in the right upper corner of each panel. Abbreviations of species names: Ar = *Arrhenatherum*; Lo = *Lolium*; Al = *Alopecurus*; Po = *Poa*; Ag = *Agrostis*; El = *Elytrigia*.

competitive ability as predicted by our third hypothesis

In contrast, the competitive change hypothesis (Tilman 1988; Taylor et al. 1990; Suding & Goldberg 2001) seemed to offer a better explanation for the observed changes in flooded mixtures. We noticed a significant change in species hierarchy of competitive abilities after flooding, indicating that the way in which flooding affects the response to competition is species-specific. Particularly surprising was the finding that 40 days of flooding resulted in significantly stronger, rather than weaker, competition on *Alopecurus* during the second year (Fig. 2). More intense competition after disturbance has been assumed before (Chesson & Huntly 1997), but to our knowledge this is the first experimental evidence.

The lack of competitive release through flooding contradicts earlier studies along hydrological gradients,

demonstrating displacement of weak competitors to the lowest ends of freshwater depth gradients (Grace & Wetzel 1981) and salt marshes (Bertness 1991; Pennings & Callaway 1992). However, along these gradients flooding operates as a stress factor (*sensu* Grime 1977) because there is a consistent constraint on productivity at the lowest positions. Floods in river forelands, as simulated here, operate more like disturbance (*sensu* Grime 1977; Huston 1979; Tilman 1988) because they occur as occasional interruptions of terrestrial conditions creating bare soil due to mortality of existing vegetation (Pollock et al. 1998; Vervuren et al. 2003).

Our measurements of competition at different periods after the flooding event indicated a gradual return of competitive effect to non-disturbed levels that was completed at the end of the second year. Given the limited time span of reduced competition, a flooding tolerance mechanism that has evolved at the expense of competitive ability may provide an unfavourable strategy for persistence. As shown here, *Agrostis* gained competitive superiority immediately after flooding and had maintained a high abundance even after the other species had fully recovered. Hence, traits that increase competitive ability after disturbance may more effectively prolong persistence in irregularly flooded habitats.

Increased competitive ability of Agrostis and a concomitant decrease for Alopecurus suggests clonal growth form as an important trait determining competitive ability after flooding. The long above-ground runners of Agrostis may be advantageous in open vegetation because they enable fast colonization of empty sites (Schmid & Harper 1985; Fahrig et al. 1994; Humphrey & Pyke 1998), a mechanism that may consequently confer long-term advantages if competing species have similar resource requirements (Wedin & Tilman 1993). Alopecurus lacks the possibility for fast colonisation of open patches because it is a tussock species with tightly aggregated ramets, a growth form that only provides competitive superiority in closed vegetation (Schmid & Harper 1985; Fahrig et al. 1994; Humphrey & Pyke 1998). Mode of lateral expansion may also explain why Agrostis was more successful in flooded mixtures than Elytrigia. Although the latter was more tolerant to flooding it is a rhizome species and therefore probably less well equipped to trace and occupy open patches (de Kroon & Hutchings 1995). Benefits of above-ground runners after flooding are also suggested by dominance of stoloniferous species such as Agrostis, Ranunculus repens and Potentilla anserina, at the lower elevated parts of natural flood-plains (Sýkora et al. 1988; Blom & Voesenek 1996).

## Conclusions

Species ranges along flooding gradients are assumed to reflect increased flooding tolerance towards lower positions and increased competitive ability towards higher positions (Keddy 1984; Blom & Voesenek 1996). Although flooding tolerance of our studied species corresponded to their lower limits in river flood-plains, competitive ability did not seem to determine their upper limit. Other factors, such as drought tolerance (Silvertown et al. 1999) should therefore also be considered when seeking for explanation of upper limits along flooding gradients. If competitive ability and flooding tolerance both affect distribution along flooding gradients they may even act in concert, because high disturbance tolerance in combination with traits that enhance competitive ability after flooding seemed to provide the most effective strategy for persistence in flood-disturbed sites.

These conclusions may apply to a broader range of plant communities because many other agents of disturbance occur as occasional, large-scale events and because most of the dominant species in herbaceous vegetation are clonal.

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