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# Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species

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## Abstract

Past research has provided compelling evidence that variation in flooding duration is the predominant factor underlying plant species distribution along elevation gradients in river floodplains. The role of seasonal variation in flooding, however, is far from clear. We addressed this seasonal effect for 10 grassland species by testing the hypothesis that all species can survive longer when flooded in winter than when flooded in summer. We carried out an inundation experiment under simulated conditions of summer and winter flooding in the greenhouse. The results showed that all species survived longer under winter floods than under summer floods. However, responses upon flooding were species-specific. All summer flood-tolerant species had high tolerance for winter floods as well, but summer flood sensitive species survived either a little longer, or dramatically longer when flooded under simulated winter conditions. Next, we examined whether winter or summer survival best predicted the lower distribution limits of the species as measured in a natural flooding gradient after an extremely long winter flood. We found a strong significant relationship between the lower distribution limits of species in the field and their tolerance to summer floods, although we measured the lower limits 14 years after the latest major summer flood. In contrast, no such significant relationship existed with species tolerance to winter floods. Some relatively intolerant species occurred at much higher floodplain elevations as was expected from their tolerance to winter inundation in the experiments. This suggests that zonation patterns as created by occasional summer floods may be maintained for a long time, probably due to the limited ability of species to re-colonise lower positions in the floodplain.

## Introduction

Flooding is the predominant environmental factor determining plant distribution in river floodplains. It indirectly determines soil composition through erosion and sedimentation (Day et al., 1988; Henry et al., 1996) and directly affects plant growth by reducing oxygen and light availability (Setter et al., 1997). Tolerance to the direct effects of flooding strongly differs among species and these differences are reflected by species zonation along elevation gradients in river floodplains (Lenssen & de Kroon, 2005). Here, the most tolerant species dominate the lower, frequently flooded positions, whereas intolerant species are restricted to the highest elevations of the floodplain (Squires & Van der Valk, 1992; Carter & Grace, 1990; Sand-Jensen & Frost-Christensen, 1999; He et al., 1999; Vervuren et al., 2003; Van Eck et al., 2004). This tight correlation between flooding tolerance and elevational position indicates that tolerance may be an important tool to predict species responses to changes in river flooding regimes as a consequence of global warming, canalization or floodplain excavation.

However, before accurate predictions can be made it may be necessary to gain further understanding of how various components of the flooding regime affect a species tolerance and how this in turn determines a species elevational distribution in floodplains. For instance, it has clearly been shown that sediment load of the flood water decreases plant survival by reducing light availability of submerged plants (Vervuren et al., 2003; Mommer et al., 2005). Season may be an equally important component of flooding regime, particularly in temperate zones where seasonal variation has a profound impact on water temperature and annual plant growth cycles.

Field observations and experiments indicate dramatic impacts of floods during the growing season (hereafter referred to as summer) on species' lower distribution limits, i.e. species' lowest position along the flooding gradient (Sykora et al., 1988; Vervuren et al., 2003; Van Eck et al., 2004). Winter floods have always been assumed to exert little direct effects, either because plants may be metabolically inactive during winter (Klimesová, 1994; Siebel, 1998), the low water temperature reduces respiration (Van Eck et al., 2005a) or because of relatively high oxygen concentration in cold water (Pedersen et al., 1998). Accordingly, the few available experiments have demonstrated a mild impact of winter floods, although these studies were limited to three species at most (Klimesová, 1994; Siebel, 1998; Van Eck et al., 2005a). A broader interspecific comparison of summer and winter floods has thus far been lacking. Such experiments, however, are required to evaluate the importance of the seasonal component of flooding regime, because observations have indicated that some summer flood-intolerant species are also sensitive to winter floods (Studer-Ehrensberger et al., 1993; Crawford et al., 2003; Crawford, 2003). Moreover, winter floods may be more important for field distribution because, at least in most rivers of the temperate zone, these will be more frequent and of longer duration due to excess rainfall and melting snow during winter and early spring (Day et al., 1988; Breen et al., 1988; Nilsson et al., 1991; Vervuren et al., 2003).

To gain further understanding of the role of the seasonal component of a river's flooding regime we extended the comparison of summer and winter flooding to 10 grassland species. We first tested the hypothesis that all species are less tolerant to summer flooding and that flooding during winter will enhance tolerance for all species with a similar magnitude, i.e. that the effect of season on tolerance is not species specific. Next, we tested the hypothesis that field distribution of floodplain species after a relatively extreme winter flooding would reflect their tolerance to winter floods. We tested these hypotheses because we assumed that the seasonal component of flooding regime would only be important if it changes the hierarchy of species tolerances. Only then may winter floods be expected to produce a different zonation pattern than summer floods. As a measure of flood tolerance we estimated $LT_{50}$, the flooding duration (Lethal Time) after which 50% of the plants had died (Vervuren et al., 2003). Earlier work has shown that $LT_{50}$ is the measure of flood tolerance that best predicts elevational distribution in floodplains (Van Eck et al., 2004).

## Materials and methods

### *Plant material and pre-treatments*

The impact of simulated summer and winter floods on species survival was investigated for 10 grassland species that inhabit different floodplain elevation ranges along the lower Rhine. The following species were selected: *Alopecurus pratensis* L., *Arrhenatherum elatius* (L.) J. and C. Presl, *Daucus carota* L., *Elytrigia repens* (L.) Nevski, *Festuca rubra* L., *Medicago falcata* L., *Plantago lanceolata* L., *Rumex acetosa* L., *Rumex crispus* L. and *Rumex thyrsiflorus* Fingerh. All species are relatively long-lived (hemi cryptophytes with winter buds just below the soil surface) and therefore likely to encounter flooding during the winter as adults. Seeds were collected in 1996 and 1998 from single populations in floodplain grasslands along the river Waal, the main and free flowing branch of the river Rhine in the Netherlands, and stored at room temperature under dry and dark conditions.

Seeds were germinated on moist filter paper in petri dishes and placed in a growth cabinet (12 h 25 $\mu$mol $m^{-2}$ $s^{-1}$ PPFR (Philips TL33), 25 °C; 12 h dark, 10 °C). In October 1999, germinated seeds were individually transferred into

800 ml pots on a mixture of sand and clay (1:1 v/v) and placed in a cold greenhouse. Light and temperature in this greenhouse followed outdoor conditions because lamps and heating system were switched off. In April 2000, the plants were placed outside the greenhouse for the summer and autumn period. Plants were watered with tap water when necessary and fertilized four times during the growth period with half strength modified Hoagland nutrient solution (Johnson et al., 1957).

### *Seasonal simulation*

Winter and summer flooding were simulated with respect to both phenological stage and water temperature. To simulate winter and summer season as closely as possible, plants assigned to the summer flooding were placed inside the greenhouse (minimum temperature 20 °C, 16 h daylight of at least 100 $\mu$mol m$^{-2}$ s$^{-1}$ as provided by additional light from growing lamps) in September 2000, 6 weeks before the start of the experiment to allow acclimation to summer conditions. To allow gradual acclimation to winter conditions, plants assigned to the winter flooding were left outdoors from September 2000–November 2000.

To estimate LT$_{50}$, we measured survival after different flood durations in simulated winter and summer conditions. In November 2000, the plants were placed in basins (diameter 1.8 m; depth 1.0 m) in the greenhouse and completely submerged in tap water of either about 20 °C (measured range 18–20 °C) or about 8 °C (measured range 5–10 °C) hereafter referred to as summer and winter treatment, respectively. Minimum and maximum water temperatures were measured weekly in each basin, using standard thermometers. There were 10 (species) $\times$ 3 (replicates) $\times$ 8 (sampling dates) = 240 plants in each basin. This resulted in a density that was low enough to prevent mutual shading. As each plant was also growing in an individual pot any form of belowground competition can be ruled out.

The basins consisted of metal rings coated with pond-foil at the inner side. The water level was fixed at 80 cm above the soil surface in the pots, to avoid restoration of leaf–air contact due to shoot elongation or leaf floating of some species. All basins were provided with a thermo-stated electric heating system at the bottom underneath the foil. Temperatures of the summer basins were kept at 20 °C. Temperature in the winter basins followed the temperatures outside the basins. Only if the temperatures in the winter basins dropped below 0 °C, it was warmed up to a maximum temperature of 6 °C. To prevent the establishment of temperature gradients in all basins a pump gently circulated the water. The basins were covered with a shade cloth to simulate the high sediment load that accompanies floods in river areas and that strongly diminishes light transmission at even a few centimetres of water depth (Vervuren et al., 2003).

Light quantities were measured weekly in each basin at the water surface and at plant level using a LI-COR (Lincoln, Nebraska) photometer (model LI-18513) with an underwater quantum sensor (LI-192SB). Average light attenuation in the water fluctuated during the experimental period between 80 and 95% of incident radiation. In the summer flooding treatment no additional light was supplemented to the basins. Therefore, tolerance to simulated summer flooding may be slightly underestimated, especially in flood-tolerant species. Relatively flood-sensitive species may be less affected since those species hardly benefit from high irradiances when submerged (Vervuren et al., 1999).

Plants were taken out of the basins at intervals that would allow a reliable fit of survival against flooding duration (Vervuren et al., 2003). Therefore, we used shorter time intervals initially so that survival of intolerant species could be accurately determined.

Simulated winter and summer treatments were each replicated in four basins. After 7, 14, 21, 28, 42, 63, 84 and 104 days of submergence three plants per species and seasonal status were taken out of each basin (in total 12 plants per species and seasonal treatment at each sampling date). A plant was considered to have survived if re-growth was noticeable within a maximum period of 1 month after emergence. To provide optimal conditions for recovery the plants were placed in a heated greenhouse (minimum air temperature 20 °C).

### *Field data*

To test our second hypothesis, stating that species elevational distribution after an extreme winter flooding reflects the species tolerance to winter flooding, we collected field data in July and August of 2001 at two floodplain locations along the river Waal: Ewijkse Waard (51° 58′ N 5° 45′ E) and Klompenwaard (51° 53′ N 6° 01′ E). In the winter of 2000/2001 flooding was relatively severe. For instance at 11.50 m above sea level, the lower limit of perennial grassland, flooding lasted for 7 weeks, whereas the average winter floods during the preceding 30 years lasted for 5.3 weeks. At this position, summer floods are usually absent (Vervuren et al., 2003); the last flooding events occurred in June and August 1987 and these lasted for 37 and 10 days, respectively.

At both floodplain sites grasslands were present with extensive grazing by cattle and horses. At Ewijkse Waard five transects were placed and at Klompenwaard one, perpendicular to the water line. In each transect vegetation data were recorded by determining the presence or absence of the selected species in sample plots of $0.45 \times 0.45$ m that were established on contour lines at 0.10 m elevation intervals along the transect. Each contour line contained 10-sample plots except one transect at Ewijkse Waard that encompassed five sample plots. Distance between the plots on a contour line was at least 2 m. Distance between transects in Ewijkse Waard was at least 50 m. The elevations of the contour lines were determined with a surveyor's level. To allow comparison between the different sites and transects, all elevations mentioned in this paper refer to elevations above sea level as standardized to Lobith gauge station. Contour lines ranged from approximately 10–14 m above sea level.

### *Statistical analysis*

Plant survival under water was analyzed using the SAS procedure LIFEREG (SAS Institute, 2001) with the Weibull model as the baseline function (Vervuren et al., 2003) and block (nested within season), season, species and interactions as covariates. We then calculated ratios of mean deviance changes, which approximately followed the F-distribution (McCullagh & Nelder, 1991) and will hereafter be referred to as Quasi *F*-values. Mean deviances allowed us to test differences between simulated seasons against variation among blocks and to treat species and block as random factors and season as a fixed factor. For each species and seasonal treatment, we subsequently estimated flooding tolerance by computing the median lethal time ($LT_{50}$; the flooding duration) at which 50% of the plant individuals from a given species had died) on the basis of Weibull equation parameters (Vervuren et al., 2003).

The lower field distribution limits of species along the flooding gradient were expressed as 10th percentile values based on species' frequency in the transects. For these analyses all species were included as far as sufficient field distribution data were available. At least five points are required to compute 10th percentile values (SPSS version 10.1). Since *Medicago falcata*, *Daucus carota* and *Rumex acetosa* were not present or only present in a few sample plots they were excluded from the analysis.

Relations between species' distribution and the experimentally obtained values for $LT_{50}$ in simulated winter and summer floods were determined by correlation analysis (SPSS version 10.1).

## Results

All species survived longer in the simulated winter floods than in the simulated summer floods (Fig. 1). However, the magnitude of the effect of the simulated flooding season was strongly species-dependent as indicated by the Species×Season interaction (Table 1). Some species survived only a little longer in the simulated winter flood than in the simulated summer flood (i.e. *Medicago falcata*, *Plantago lanceolata*, *Arrhenatherum elatius* and *Daucus carota*), but for others with relatively low tolerance to summer floods, survival was dramatically increased (i.e. *Rumex acetosa*, *Alopecurus pratensis*, *Rumex thyrsiflorus* and *Festuca rubra*) (Fig. 1). Survival of summer flood-tolerant species (i.e. *Elytrigia repens* and *Rumex crispus*) was also extended under winter floods.

The distributions of the species along the flooding gradient differed widely (Fig. 2). Likewise, the lower limits (10th percentile values) depended on the species and ranged from 11.35 to 13.27 m. For some species the lower limits were situated at relatively high elevations corresponding with relatively low flood durations (e.g. *Arrhenatherum elatius*), whereas others occurred at

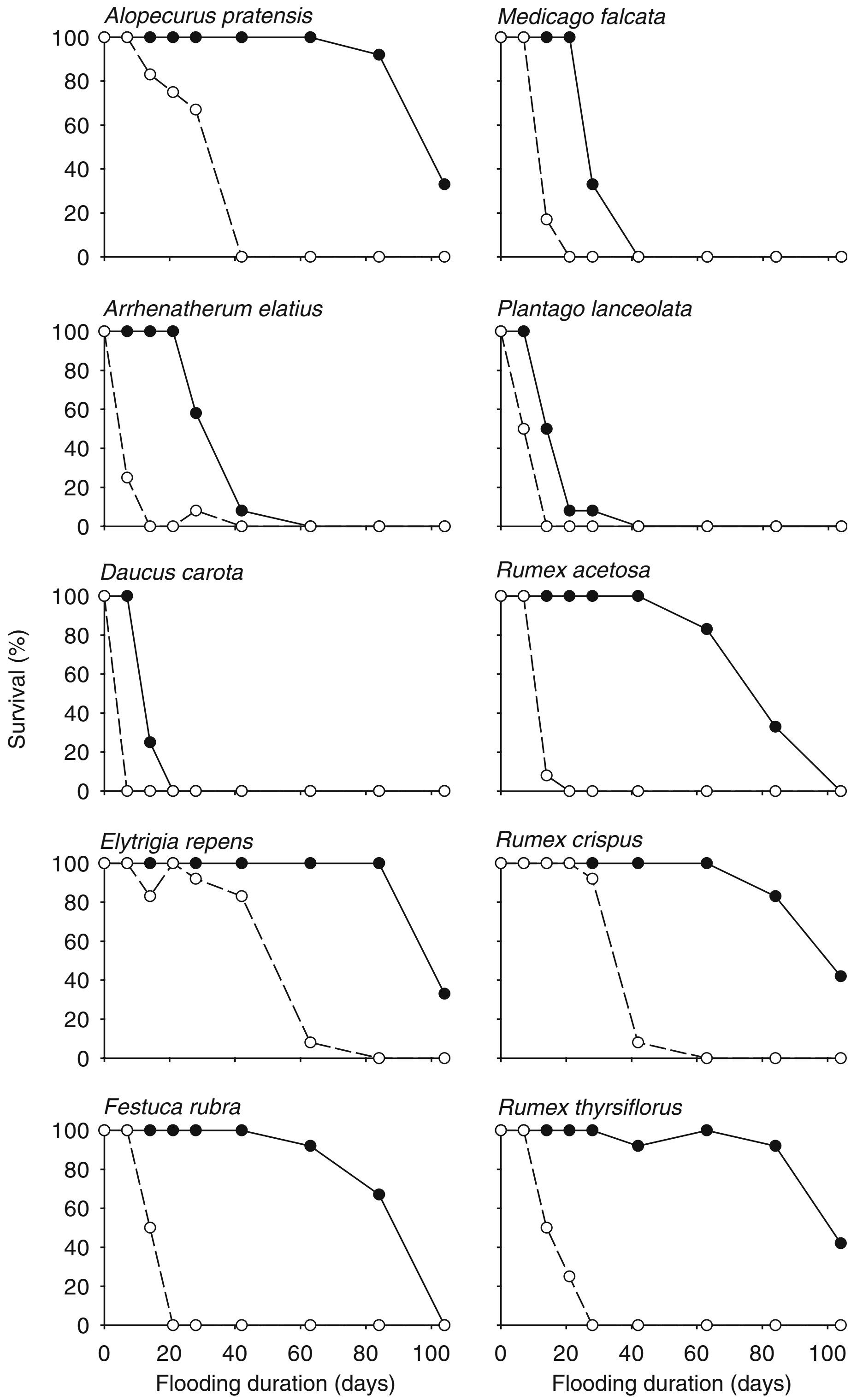

*Figure 1*. Relationship between flooding duration and survival (based on 12 replicate plants per flooding duration) of 10 river floodplain grassland species in simulated winter (closed symbols) and simulated summer floods (open symbols).

*Table 1.* Analysis of deviance for survival time under influence of species, simulated flooding season and block (season)

| Source of variation | df (effect, error) | Mean deviance | Quasi *F*-value |
|---|---|---|---|
| Block(season) | 6, 1895 | 0.09 | 0.12 |
| Season | 1, 6 | 0.00 | 0.00 |
| Species | 9, 54 | 4.27 | 21.68*** |
| Season×Species | 9, 54 | 1.16 | 5.90*** |
| Species×Block(season) | 54, 1895 | 0.20 | 0.25 |
| Residual | 1895 | 0.77 | |

Mean deviance, Quasi *F*-values and significance levels are presented; df, degrees of freedom (effect, error); ***, $p < 0.001$.

much lower elevations corresponding with longer flood durations (e.g. *Rumex crispus*). *Elytrigia repens* was present at relatively high frequencies along the whole flooding gradient. There was a highly significant negative correlation between species tolerance to summer flooding and the lower distribution limits along the flooding gradient (Fig. 3a) indicating that summer flood intolerant species were restricted to higher elevations in the floodplain (e.g. *Arrhenatherum elatius*) while more summer flood tolerant species (e.g. *Elytrigia repens* and *Rumex crispus*) occurred at lower elevations. Species with intermediate tolerances to summer floods occurred at elevations in the mid-range of the flooding gradient (e.g. *Alopecurus pratensis*).

In contrast, the correlation between species' tolerance to winter floods and their lower distribution limits along the flooding gradient was not significant (Fig. 3b). The lower distribution limits of a number of winter flood tolerant species ranged

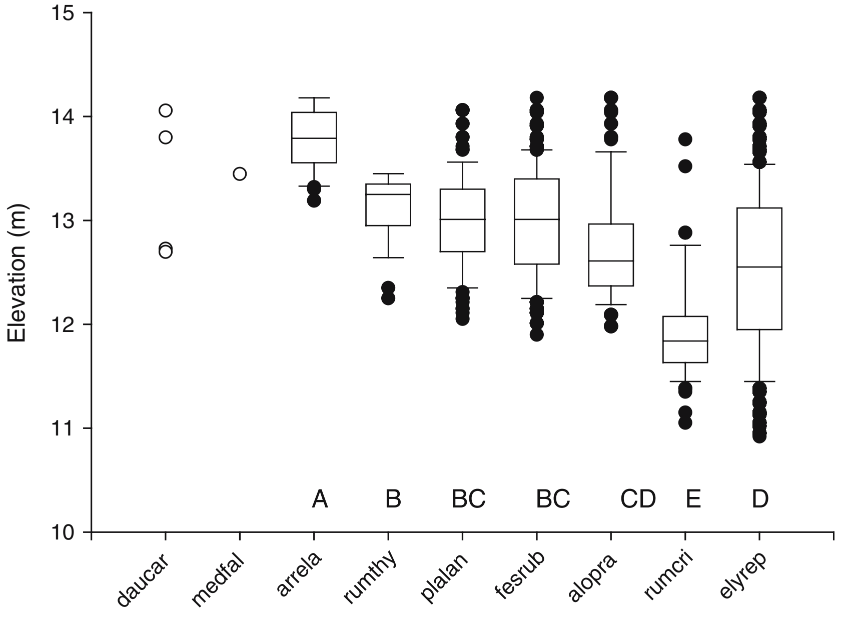

*Figure 2.* Species distribution along the flooding gradient based on six transects at two floodplain sites along the river Rhine in the Netherlands after the winter flood of 2000/2001. The end of the boxes defines the 25th and 75th percentiles, with a line at the median and error bars defining the 10th and 90th percentiles. Circles define data points beyond the 10th and 90th percentiles. For *Medicago falcata* and *Daucus carota* there were less than the minimum required number of data points (indicated by open circles) to compute a reliable set of percentiles and therefore excluded from analysis. *Rumex acetosa* was not observed within the sample plots along the transects. Species abbreviations: alopra = *Alopecurus pratensis*, arrela = *Arrhenatherum elatius*, daucar = *Daucus carota*, elyrep = *Elytrigia repens*, fesrub = *Festuca rubra*, medfal = *Medicago falcata*, plalan = *Plantago lanceolata*, rumcri = *Rumex crispus* and rumthy = *Rumex thyrsiflorus*. Letters above the species names denote the Tukey-grouping after one-way ANOVA; species with the same letter have the same distribution along the flooding gradient ($p < 0.05$).

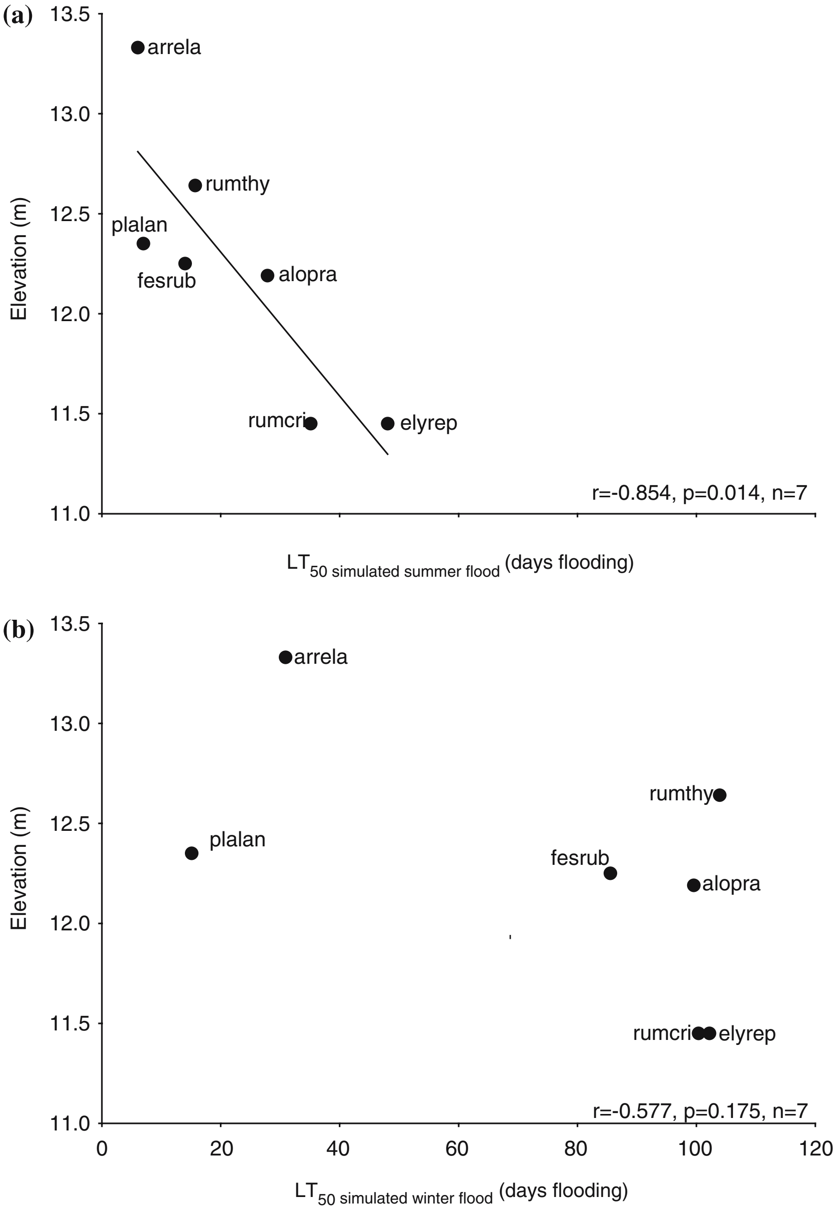

*Figure 3*. Relationship between species' lower distribution limits along the flooding gradient of the river Rhine in 2001 and the experimentally obtained values for flooding tolerance ($LT_{50}$) in (a) simulated summer floods and (b) simulated winter floods. For species abbreviations see Figure 2.

from low to high floodplain elevations whereas two very intolerant species (*Arrhenatherum elatius* and *Plantago lanceolata*) occurred only relatively high on the gradient.

We translated the species' lower distribution limits to the flooding durations in the winter of 2000/2001 and the summer of 1987 and correlated these flooding durations with their tolerance to simulated winter and summer floods, respectively. The flooding durations in the summer of 1987 and the winter of 2000/2001 were strongly correlated ($r^2 = 0.89$, $p < 0.001$) due to the strong relationship between flooding duration and elevation along the flooding gradient. Species' tolerance to simulated summer floods was highly correlated with the flooding durations at the lower distribution limits in the summer of 1987, the last severe summer flood in the study area (Fig. 4a). The flooding duration during the winter of 2000/2001 at species' lower distribution limits was not significantly correlated with their tolerance to simulated winter floods (Fig. 4b). Not all species occurred at elevations that were expected on the basis of their tolerance to simulated winter floods. Most striking was that some species that appeared to be tolerant to simulated winter floods (*Festuca rubra*, *Alopecurus pratensis* and *Rumex thyrsiflorus*) had their lower limits at positions that were only shortly flooded in the winter of 2000/2001 (Fig. 4b). On the other hand, *Plantago lanceolata*

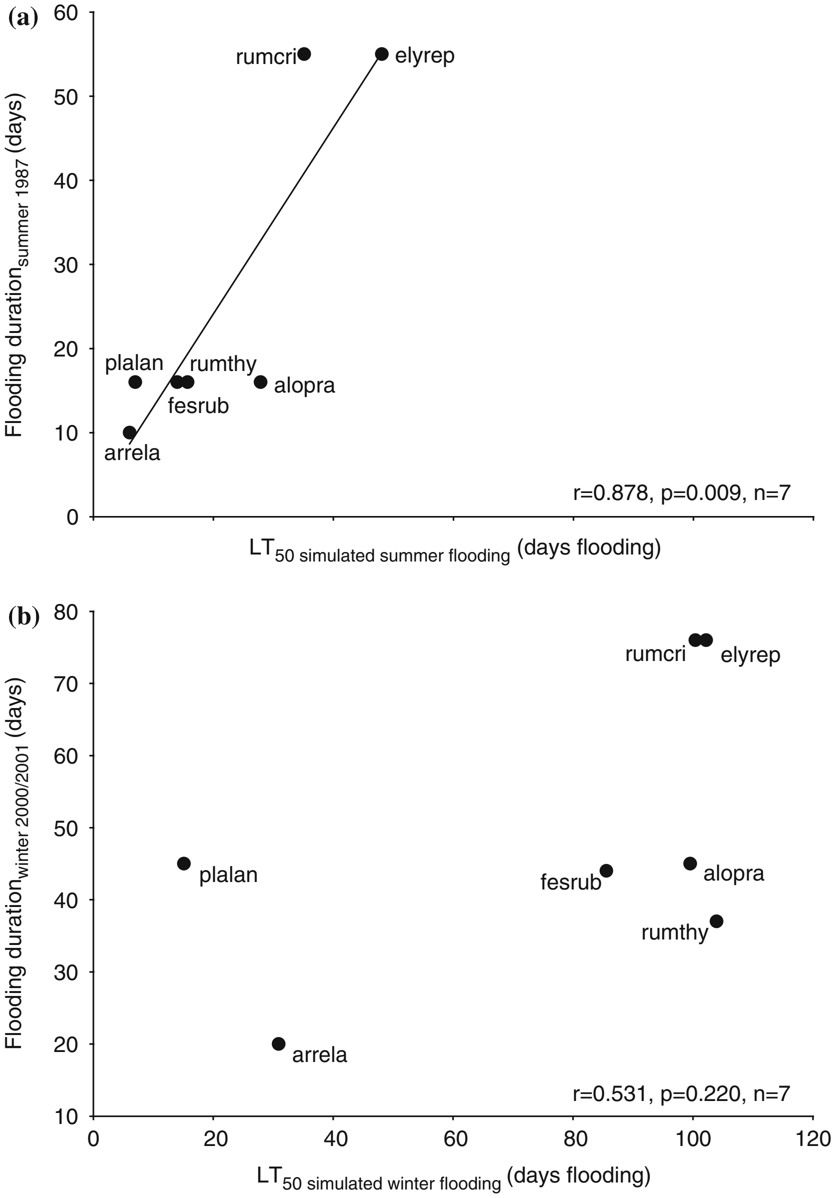

*Figure 4*. Relationship between flooding duration at species' lower distribution limits along the flooding gradient of the river Rhine in (a) the summer of 1987 and their flooding tolerance ($LT_{50}$) in simulated summer floods and (b) the flooding duration in the winter of 2000/2001 and their flooding tolerance in simulated winter floods. For species abbreviations see Figure 2.

occurred under longer flooding durations than was expected on the basis of its poor tolerance to winter floods. The very intolerant *Arrhenatherum elatius* only occurred under very short winter flooding durations, and its distribution seems to be limited by summer as well as winter flooding.

## Discussion

The tolerance of plant species to complete submergence strongly depended on the simulated season of flooding. In accordance with our first hypothesis, all 10 species survived longer under the simulated winter flood than under the simulated summer flood. Our results thus corroborate those of Klimesová (1994) and Siebel (1998) who demonstrated that floods during the winter have a lower impact on survival of *Urtica dioica* plants than floods during the growing season. However, in contrast to our first hypothesis, the magnitude by which winter flooding enhanced tolerance was species-specific (Table 1). The specific response to flooding season may be related to interspecific differences in the use of stored carbohydrates during submergence, rather than to mitigating effects of higher oxygen concentrations in cold water (Van Eck et al., 2005a). Stored carbohydrates may prolong survival when submerged (Setter et al., 1997; Laan & Blom, 1990; Crawford, 2003; Nabben, 2001). Van Eck et al. (2005a) demonstrated that *Rumex crispus* had a conservative carbohydrate use at both low and high water temperatures. *Rumex acetosa*, although able to access its reserves in the roots, had a high rate of carbohydrate respiration in warm water but this rate slowed down at lower temperatures. This decreased rate of carbohydrate depletion probably explains why this species, like *Alopecurus pratensis*, *Festuca rubra* and *Rumex thyrsiflorus*, was able to extend its survival dramatically in simulated winter flood compared to summer floods in the present experiment. Accordingly, *Daucus carota* was not able to access its belowground carbohydrate reserves (Van Eck et al., 2005a) and its tolerance was also little enhanced in simulated winter floods. Hence, the findings of Van Eck et al. (2005a) together with the results presented here suggest that only species with an ability to mobilize and respire carbohydrates when submerged are able to prolong survival of flooding outside the growing season. Species that are intolerant to flooding regardless of season, such as *Arrhenatherum elatius*, *Daucus carota*, *Medicago falcata* and *Plantago lanceolata*, probably lack a physiological mechanism for accessing carbohydrate reserves when submerged.

Because seasonal effects of flooding are species-specific it may be expected that winter floods produce a different zonation in floodplain grasslands than summer floods. Accordingly, we found that species' lower limits were not equally well correlated with tolerance to summer and winter flooding. Surprisingly, however, it was the tolerance to summer floods that best explained lower distribution limits although the last summer flood in our study area occurred more than 14 years before our field data were collected. Moreover, a severe winter flood occurred immediately before the year in which field data were recorded but, in contrast to our second hypothesis, we found no significant correlation between species' distribution and tolerance to winter floods.

Our results further suggest that only the field distribution of *Arrhenatherum elatius*, the most intolerant species, was limited by winter flooding. Based on their tolerance to winter floods, species such as *Rumex thyrsiflorus*, *Alopecurus pratensis* and *Festuca rubra* could have occurred at much lower elevations than actually found. The poor correlation between flooding tolerance and lower limits suggests that other factors than flooding tolerance may be involved in determining lower distribution limits of these species in periods without severe summer floods (Van Eck et al., 2005b). Traits determining colonization ability may control the speed of migration down the flooding gradient as other studies indicate a strong relationship between colonization ability and abundance in disturbed habitats (Van der Sman et al., 1993; Collins et al., 1995; Henry et al., 1996; Burke & Grime, 1996). *Plantago lanceolata*, although very sensitive to winter flooding, did occur at relatively low floodplain elevations, suggesting that this species may rapidly colonise empty microsites created by winter floods. In addition to dispersal, winter floods may indirectly, through erosion and sedimentation, prevent successful establishment at lower positions (Van Eck et al., 2005b).

In conclusion, we have shown that species may either be tolerant to both winter and summer flooding, considerably more tolerant to winter flooding, or intolerant to flooding regardless of season. The species-specific tolerance to winter flooding suggests that these floods may also affect species distribution along elevation gradients in river floodplains. However, as shown here for grasslands along the river Rhine, the actual zonation may bear the signature of summer floods, because these floods, although less frequent, have a more dramatic impact on plant survival.

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