Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient

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Summary

1 Competition is widely thought to be responsible for constraining species limits at the favourable ends of freshwater flooding gradients. However, field studies testing this idea rarely consider the role of competition beyond a species’ field distribution limits.

2 To test whether species distributions are, instead, constrained by physiological limits, and only narrowed by biotic interactions, we measured the effect of competition on survival and fecundity of *Rumex crispus* and *Rumex palustris* within and above their distribution range along an elevation gradient in a river floodplain.

3 Flooding reduced the fitness of both species at the lowest elevations. A decline in fitness was also noticed at the two highest elevations in control as well as in removal plots, although standing crop measurements indicated that conditions here were the most favourable.

4 Both leaf herbivore damage and likeliness of drought increased with elevation. Because herbivore damage only reinforced prevailing abiotic influences, drought appeared to be the strongest constraint at higher positions.

5 Competition merely narrowed both species’ physiological ranges by displacing them downwards from their optimum and maximum elevation. The displacement was strongest for the weak competitor *Rumex palustris*.

6 Our study provides experimental field evidence for earlier suggestions that both ends of a species niche can be defined in hydrological terms. It thus indicates that spatial variability in water availability may segregate species niches and thereby promote species richness in plant communities.

Key-words: competitive displacement, disturbance, drought, flooding, herbivory, hydrological gradients, niche, zonation

Introduction

Segregation of species ranges is a common phenomenon along flooding gradients of lakes, rivers and salt marshes (Keddy 1984; Bertness 1991; Silvertown et al. 1999). The duration and frequency of floods decrease with elevation, and the zonation of species along these gradients therefore suggests that variation in flooding regimes may be an important factor inducing specialization (Keddy 1984; Crawford 1992; Silvertown et al. 1999, 2001). There is abundant experimental evidence that occurrence at lower positions requires tolerance to flooding (Grace & Wetzel 1981; Bertness 1991; Shipley et al. 1991; Pennings & Callaway 1992; Castillo et al. 2000; Johansson & Nilsson 2002; Vervuren et al. 2003; Lenssen et al. 2004b; Van Eck et al. 2004) but it is still unclear why flood-tolerant species are excluded from higher positions of freshwater flooding gradients.

It has been proposed that biotic factors gain importance as the impact of flooding decreases with elevation (Menge & Sutherland 1976). Accordingly, a number of studies have indicated a potential role for herbivory in constraining a species’ upper limit because grazing increases with elevation (Bukker 1985; Warren 1993; Furbisch & Alban 1994; Rand 2002; Costa et al. 2003). Others have hypothesized that a trade-off between flooding tolerance and competitive ability confines each species to a certain range of the flooding gradient (Grace 1990; Keddy 1990; Crawford 1992). Species that are best able to resist suppression by interspecific neighbours under favourable conditions are restricted to the highest positions because regular floods prevent their persistence at lower sites. Conversely, highly
tolerant species are weak competitors and are therefore excluded from the more favourable, elevated positions: their realized, ecological range thus differs from their physiological range (sensu Austin 1990) because, in the absence of neighbour interactions, they would be capable of inhabiting the entire gradient (Grace 1990; Keddy 1990; Crawford 1992).

Many field studies show that competition is indeed strongest at the upper limit of a species’ realized range (Grace & Wetzel 1981; Bertness 1991; Shipley et al. 1991; Lenssen et al. 1999, 2004a; Budelsky & Galatowitsch 2000; Rand 2000). However, salt marsh studies have shown that fitness may be greater at intermediate than at higher positions even if vegetation is removed (Pennings & Callaway 1992; Bertness & Leonard 1997). Although it is generally recognized that conditions along environmental gradients may change from harsh to favourable and then to harsh again (Austin 1990; Keddy 1990) there was no decline in standing crop at the upper positions where the target saltmarsh species appeared physiologically limited. Abiotic constraints that operate independently from productivity may therefore contribute to species upper limits.

In salt marshes, limitations at higher positions are mainly due to increased soil salinity (Pennings & Callaway 1992; Bertness & Leonard 1997). Upper limits in freshwater flooding gradients are strongly related to water availability (Silvertown et al. 1999), again suggesting abiotic limitations, although we are not aware of any experimental field evidence, possibly because studies have tended to concentrate on species’ realized ranges (Shipley et al. 1991; Lenssen et al. 1999, 2004a).

A strong effect of neighbour removal at the upper realized limit is not, however, inconsistent with it being determined by abiotic factors. If competition merely modifies a species’ physiological range, it might do so by displacing a species from its physiological optimum to lower positions (Ellenberg 1953; Austin 1990). Removing the influence of neighbours will then allow a species to achieve its physiological optimum and effects of competition may therefore seem strongest at the upper boundary. A critical evaluation of the role of competition therefore requires measuring fitness with and without neighbours above the realized upper limits. If fitness remains constant or continues to increase without neighbours, competition would be the only factor responsible. However, a fitness decline in spite of neighbour removal would strongly suggest a role for abiotic stress in determining upper limits.

Here we report a field experiment on Rumex palustris (typically found at low elevations) and Rumex crispus (mid range) along a freshwater flooding gradient. We measured the effects of neighbour removal on fitness within and above the actual range of both species to test the hypothesis that only biotic factors (interspecific competition) constrain their upper ranges (Grace 1990; Keddy 1990; Crawford 1992) and that fitness of both species would therefore increase with elevation after neighbour removal. We next predicted that upper limits of the two Rumex species reflected their relative competitive ability and that R. crispus would therefore be the better competitor. To test whether environmental conditions became more favourable towards higher positions we measured standing crop and also monitored herbivore damage and soil moisture to assess their possible role along our flooding gradient.

**Materials and methods**

**SPECIES AND SITE DESCRIPTION**

Both Rumex crispus L. and Rumex palustris Sm. are monocarpic rosette species that do not start flowering before a certain minimum size has been reached. R. crispus usually sets seed in the second year after germination but may also have a longer life cycle (Akeroyd & Briggs 1983), whereas R. palustris may behave as either an annual or biennial species (Van der Sman et al. 1993). Rumex species are an important food source of the beetle Gastrophysa viridula, whose spatial distribution closely follows Rumex obtusifolius, its main host plant (Bentley et al. 1980). In our study area, the range of Rumex obtusifolius was similar to that of Rumex crispus. At higher positions of the floodplain, Rumex species may also be heavily grazed by molluscs (Voesenek 1990; J.P.M. Lenssen, personal observations).

The experiment was carried out in the Ewijkse Waard nature reserve (51°53’ N, 5°45’ E), along a branch of the lower section of the River Rhine in the Netherlands. Water discharge in the river is determined by snowmelt in the Swiss Alps and autumn and winter precipitation upstream from the study site. Flooding is therefore a common event in winter and early spring (Vervuren et al. 2003). The branch is largely isolated from the main river channel by a high river dune but is connected at one end if water level exceeds 1050 cm a.s.l. (all elevations were standardized to Lobith gauge station). Below this threshold, the water level in the branch is determined by local precipitation and evaporation. Due to its backward position relative to the main channel, water flow during flooding events is low and clay deposition therefore predominates over sand deposition or soil erosion.

Within such sheltered river forelands, the two Rumex species are normal constituents of pioneer vegetation on mudflats, as well as in grassland vegetation at higher elevations (Blom et al. 1996). Below approximately 1100 cm a.s.l. at our study site, R. palustris grows in vegetation dominated by annuals and short-lived perennials such as Bidens frondosa, Rumex maritimus, Tripleurospermum maritimum and Xanthium strumarium, whereas in its upper range (between 1100 and 1150 cm a.s.l., Fig. 1), clonal forbs such as Potentilla anserina, Potentilla reptans and Rorippa sylvestris are most abundant. The natural range of R. crispus (Fig. 1) extends upwards to positions where the perennial grasses Agrostis stolonifera and Elytrigia repens are abundant, but ends below grassland dominated by Alopecurus
pratensis, Dactylis glomerata, Lolium perenne and Poa trivialis. Extensive grazing by horses and cows has led to alternating patches of grassland perennials and grazing resistant tall forbs such as Urtica dioica and Cirsium arvense (Olff et al. 1999). Abundant thistle patches near the experimental plots kept herbivore grazers away during most of the growing season.

EXPERIMENTAL PROCEDURE

Seeds were collected in 1999 within the same river area from a single population for each species. On 28 March 2000, seeds were germinated on plastic grains moistened with tap water. Soon after germination each seedling was transplanted to a 100-mL pot filled with a 1 : 1 (volume ratio) mixture of sand and clay and further raised in a glasshouse. On 4 May 2000 seedlings with two cotyledons and two true leaves were selected and transferred to the field site.

We selected six sites with different elevational positions, i.e. 1043, 1065, 1140, 1194, 1265 and 1367 cm a.s.l., to include both the natural range of both species (indicated in Fig. 1) and elevations above this range. These positions dispersed throughout the study area and were separated by at least 20 m.

At each site we laid out two blocks (each 150 wide × 180 cm along the chosen elevation) separated by at least 2 m. To match natural habitat conditions, we placed each block within a natural population of the Rumex species found at that level, or in a grass-dominated patch at higher elevations. Each block consisted of five parallel rows with 30 cm between each row and with six planting positions in each row, also separated by 30 cm. After using a random number generator to assign each position to a combination of species and removal treatment, we planted one seedling at each position. Seedlings that died during the first 3 weeks were replaced. As we expected a higher mortality of plants with neighbouring vegetation we assigned 10 seedlings per species to control treatments and five seedlings per species to removal treatment in each block. Hence, at each site we started with 20 replicates per species for the control treatment and 10 replicates per species for the removal treatment.

Before planting, we removed above-ground vegetation and the upper 3-cm soil layer, which contained most of the roots, in positions that were assigned to the removal treatment. We cleared a circle with 15-cm diameter and also trenched the outer perimeter to a depth of c. 15 cm. To avoid damage to the target plant we did not repeat this sod-cutting and trenching after planting but instead manually weeded all regrowth within the radius at 2-week intervals during the growing season (May–September). The experiment was continued until July 2002, by which time all plants had either set seed or died.

ENVIRONMENTAL PARAMETERS

Daily measurements from a nearby gauge station in the main river channel were used to assess the water levels relative to our study site. We recorded the water level in the river branch at approximately 2-week intervals during periods when it was isolated from the main river channel.

On 4 July and 23 August 2001 (following 7-day and 4-day dry periods, respectively) we measured soil moisture content with a TRIME-FM probe P2 (IMKO GmbH, Ettingen, Germany). Values therefore reflect water availability at each site as determined by local environmental factors such as soil composition, ground water table depth and vegetation. Six measurements were taken at each site, at random positions within vegetated parts of the grids, and in July we also measured soil moisture near randomly chosen plants without neighbours.

As a measure of productivity we determined standing crop at each site in June and August of 2000 and 2001. An iron frame of 45 × 45 cm was placed at six different positions close to, but not within, the planting grids. All above-ground vegetation was clipped at ground level and dry weight was determined after drying at 70 °C for at least 48 hours.

PLANT MEASUREMENTS

At monthly intervals during the three consecutive growing seasons we counted the total number of leaves and the number of leaves that were damaged by herbivores on all plants in the vegetative phase. A leaf was considered to be damaged by herbivores if at least 25% of leaf area had been removed. These data allowed us to assess leaf herbivore damage, although only by estimation because we had not tagged individual leaves. For each individual we estimated leaf herbivore damage by calculating the ratio of the total number of damaged
leaves \((N_i)\) to the total number of leaves \((N)\), during the entire vegetative phase. The total number of (damaged) leaves was estimated by the sum of the initial number of (damaged) leaves and the additional number of (damaged) leaves at each consecutive census until the moment \((t = a)\) that plants had died or started bolting:

\[
\text{Herbivore damage} = \frac{N_{d,t=0} + \sum_{t=0}^{a} (N_{d,t} - N_{d,t-1})}{N_{va} + \sum_{t=0}^{a} (N_t - N_{t-1})}
\]

For each individual we recorded whether it had started bolting and after how many days bolting was first observed. To avoid losses through seed fall, achenes were harvested as soon as they had formed after flowering. Following earlier work on monocarpic plants (Waser et al. 2000), we calculated individual fitness for each plant that flowered as \(\lambda\), the time-specific seed production, by solving the equation

\[
1 = \sum_{t=1}^{a} F_t \cdot \lambda^{-t}
\]

where \(F_t\) indicates age-specific seed production from the first year until the plant’s maximum life span \(\omega\) (McGraw & Caswell 1996). Because both our Rumex species were monocarpic the equation could be simplified to

\[
1 = F_t \cdot \lambda^{-t}
\]

where \(t\) refers to the year of flowering, ranging from 1 to 3 in our study.

### Results

#### ENVIRONMENTAL PARAMETERS

Standing crop tended to increase with elevation as shown by the significantly positive relationships between these variables in June of the first growing season and August of the second growing season and the marginally significant positive relationship in June of the second growing season. By the end of the first growing season, however, the relationship observed earlier in the year had disappeared and a one-way ANOVA that compared standing crop among elevations did not indicate any difference between elevations \((F_{5,24} = 1.61, P = 0.19)\).

At all elevations, water level was below the soil surface during most of the first and second growing seasons (Fig. 1). All plots were flooded in the winter of 2000/2001, but duration ranged from more than 7 months at the lowest elevations to only a few days at the highest positions (Fig. 1).

At both measurement dates, soil moisture content significantly decreased with elevation (Table 1), indicating that soils were drier at higher positions, at least after periods without rainfall. As shown by the measurements in July 2001, moisture content was usually higher in vegetated soil (Table 1), but there was only a significant main effect of vegetation removal \((F_{1,49} = 5.13, P = 0.02)\) and no significant interaction \((F_{5,49} = 1.52, P = 0.20)\). This indicates that, in spite of neighbour removal, water availability decreased with elevation. Moreover, the effect of vegetation removal on water limitation at a given elevation was small compared with the variation found between similar neighbour treatments at different elevations.

#### HERBIVORY

As shown by the significant main effect of species (Table 2) there were consistent differences in herbivory
between R. crispus and R. palustris, probably because R. crispus suffered more damage (Fig. 2). Leaf herbivore damage also tended to increase with elevation (Fig. 2), although this elevation effect depended on the species under consideration (Table 2). This interaction may have been due to the steeper increase in herbivore damage towards higher elevations for R. palustris (Fig. 2).

Table 2 Statistical analyses of effects of elevation (linear and quadratic terms), species and neighbour removal on herbivory (proportion of damaged leaves), vegetative period (number of days until flowering), individual λ (time-specific seed production) and survival during the first growing season (‘summer’) and the following winter. Table entries give degrees of freedom (d.f.: effect, error; error d.f. estimated with Satterwaithe approximation) and $F$-values for fixed factors, estimated after fitting all random terms, and change in deviance for random factors. Symbols and abbreviations: $\dagger P < 0.1$ (marginally significant), $* P < 0.05$, $** P < 0.01$, $*** P < 0.001$, ND = not determined

### Standing crop, year one

<table>
<thead>
<tr>
<th>Elevation</th>
<th>1043</th>
<th>1065</th>
<th>1140</th>
<th>1194</th>
<th>1265</th>
<th>1367</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>98 ± 12</td>
<td>152 ± 22</td>
<td>347 ± 32</td>
<td>273 ± 26</td>
<td>227 ± 25</td>
<td>238 ± 28</td>
<td>0.460**</td>
</tr>
<tr>
<td>August</td>
<td>422 ± 68</td>
<td>617 ± 46</td>
<td>527 ± 44</td>
<td>518 ± 59</td>
<td>537 ± 36</td>
<td>488 ± 50</td>
<td>0.070</td>
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</table>

### Standing crop, year two

<table>
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<th>Elevation</th>
<th>1043</th>
<th>1065</th>
<th>1140</th>
<th>1194</th>
<th>1265</th>
<th>1367</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>ND</td>
<td>ND</td>
<td>84 ± 4</td>
<td>47 ± 2.0</td>
<td>71 ± 5.0</td>
<td>97 ± 12</td>
<td>0.369†</td>
</tr>
<tr>
<td>August</td>
<td>59 ± 2</td>
<td>213 ± 14</td>
<td>185 ± 8.4</td>
<td>177 ± 17</td>
<td>228 ± 10</td>
<td>288 ± 25</td>
<td>0.698***</td>
</tr>
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</table>

### Soil water content

July

<table>
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<th>Elevation</th>
<th>1043</th>
<th>1065</th>
<th>1140</th>
<th>1194</th>
<th>1265</th>
<th>1367</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>388 ± 16</td>
<td>414 ± 5</td>
<td>228 ± 17</td>
<td>184 ± 37</td>
<td>184 ± 5</td>
<td>64 ± 12</td>
<td>–0.717***</td>
</tr>
<tr>
<td>Closed</td>
<td>375 ± 14</td>
<td>418 ± 1</td>
<td>250 ± 18</td>
<td>270 ± 14</td>
<td>201 ± 20</td>
<td>156 ± 29</td>
<td>–0.844***</td>
</tr>
<tr>
<td>August</td>
<td>337 ± 25</td>
<td>353 ± 12</td>
<td>258 ± 13</td>
<td>308 ± 6</td>
<td>278 ± 6</td>
<td>286 ± 6</td>
<td>–0.390***</td>
</tr>
</tbody>
</table>

### Survival (summer)

<table>
<thead>
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<th>Species</th>
<th>1043</th>
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<th>1140</th>
<th>1194</th>
<th>1265</th>
<th>1367</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. crispus</td>
<td>0.390***</td>
<td>0.844***</td>
<td>0.717***</td>
<td>1.111</td>
<td>0.13</td>
<td>1.111</td>
<td>0.20</td>
</tr>
<tr>
<td>R. palustris</td>
<td>0.369†</td>
<td>0.844***</td>
<td>0.717***</td>
<td>1.111</td>
<td>0.13</td>
<td>1.111</td>
<td>0.20</td>
</tr>
</tbody>
</table>

### Survival (winter)

<table>
<thead>
<tr>
<th>Species</th>
<th>1043</th>
<th>1065</th>
<th>1140</th>
<th>1194</th>
<th>1265</th>
<th>1367</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. crispus</td>
<td>1.103</td>
<td>0.14</td>
<td>0.14</td>
<td>1.103</td>
<td>0.14</td>
<td>1.103</td>
<td>0.14</td>
</tr>
<tr>
<td>R. palustris</td>
<td>1.103</td>
<td>0.14</td>
<td>0.14</td>
<td>1.103</td>
<td>0.14</td>
<td>1.103</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Survival in the first growing season seemed strongly enhanced by vegetation removal, although this effect was restricted to certain blocks and species dependent (Table 2, Fig. 3). We found no significant effect of elevation on survival during the first growing season, although
relatively few plants of *R. palustris* with neighbours survived at the highest elevation (Fig. 3).

At the end of the first growing season, all *R. palustris* without vegetation at the two lowest elevations had already started to flower, whereas all individuals with neighbouring vegetation at the highest elevation had died (Fig. 3). As a consequence, a full factorial model for winter survival could not be fit (Table 2). As indicated by the significant quadratic term for elevation (Table 2), survival during winter decreased both towards higher and lower elevations (Fig. 3). Decreased survival at lower elevations reflects the effects of flooding because flooding duration decreased with elevation during the winter season (Fig. 1). Hence, the lack of a significant elevation–species interaction (Table 2) indicates that both species were equally flood tolerant.

**REPRODUCTION**

All plants bolted earlier if vegetation was removed, but the relative effect of vegetation removal differed between species (Table 2). *R. crispus* with neighbouring vegetation started bolting after 600.1 ± 35.8 days vs. 443.0 ± 30.4 days without, whereas *R. palustris* bolted earlier, and the impact of vegetation was, in relative terms, larger (165.8 ± 36.4 days vs. 74.5 ± 2.4 days; all means ± SE, *n* = 17–29, pooled across sites). Elevation also affected species responses to neighbour removal (Table 2), but never induced a reversal of species-specific removal effects on duration of vegetative period (data not shown).
Due to high mortality of seedlings at the lowest and highest elevations, the impact of competition on individual $\lambda$ could not be measured along the entire gradient (Fig. 4). Within the studied range, individual $\lambda$ was two orders of magnitude higher for *R. palustris* than for *R. crispus* (Fig. 4). This indicates that *R. palustris* had an intrinsically higher yearly seed output although the different letters indicate significant differences between no-neighbour treatments at different elevations (least significant difference method, $P < 0.05$).

\[ \text{Relative effects of herbivory and elevation on fitness} \]

The analysis that included both elevation and herbivory as predictor variables (Table 3) revealed that probability of flowering varied unimodally along the elevation gradient, although this pattern also depended on the amount of herbivory and on species identity (Table 3). A subsequent forward multiple logistic regression for each species separately (with both removal treatments pooled) indicated, for *R. crispus* only, a significant positive relationship for the interaction of herbivory and the linear term of elevation (coefficient = 0.32; Wald $\chi^2 = 18.68; P < 0.001$). This suggests that *R. crispus* was more likely to reach the flowering stage at higher elevation, particularly if it was also grazed. In the case of *R. palustris*, multiple regression analysis indicated a negative interaction between herbivory and the quadratic term of elevation (coefficient = -0.0438; $P < 0.001$). Hence, this species was most likely to reach the flowering stage at intermediate elevational positions, with the decreasing trend towards higher positions reinforced by herbivore damage.

Variation in individual $\lambda$ was explained by linear terms of elevation, although again depending on the species under consideration (Table 3). Subsequent multiple regression analysis indicated that this species-dependent
Upper boundaries on flooding gradients

effect was due to a lack of significance of the interaction term for *R. crispus* (coefficient = −2.78; $F = 1.03; P = 0.315$) and a significantly negative relationship for *R. palustris* (coefficient = −606.437; $F = 4.99; P = 0.028$). The latter finding again indicates that negative effects on *R. palustris* at higher elevational positions may be reinforced by herbivory.

**Discussion**

We tested the hypothesis that competition alone excludes species from the more favourable, higher positions along a natural freshwater flooding gradient. We found that competition strongly decreased survival during the first growing season, but this effect did not increase towards higher elevations (Table 2). Moreover, in control as well as in removal plots, all surviving seedlings produced fewer seeds at the two highest positions (Fig. 4) where standing crop indicated that conditions were more favourable (or at least equally favourable) than at lower positions (Table 1). Therefore, our first prediction that competition alone would constrain fitness at the upper end of our flooding gradient was not supported for either species, suggesting that some abiotic factor (or another biotic factor) related to elevation may also be involved.

**ABIOTIC FACTORS**

Among the alternative factors affecting plant distribution, water limitation seems the most likely candidate. At least after extended periods without rainfall, soil moisture was inversely related to elevation and our data therefore strongly suggest that water limitation is more likely at higher positions of the flooding gradient. Water limitation also seemed to be increased by neighbour removal (Table 1) and water content values at the optimum elevation for plants without neighbours were roughly similar to values for plants in closed grass turfs at the highest elevation. This indicates that competition may further decrease the ability to tolerate dry soils, probably by hampering formation of a larger and deeper root system (Reader et al. 1992).

Standing crop data (Table 1) indicated no general resource limitation towards higher elevations, suggesting that our *Rumex* species may be particularly sensitive to drought. This may be due to their high amount of aerenchyma (Laan et al. 1989), internal ventilation channels that improve oxygen availability in flooded plants but enhance transpiration losses in dry conditions (Keeley 1979). Decreased tolerance to drought by flooding tolerant species was also demonstrated in glasshouse studies (Carter & Grace 1990; Parolin 2001) and strongly suggested by field observations (Silvertown et al. 1999).

While water limitation was most probably determining fitness at the highest positions, flooding was the most important environmental force at the lowest positions. Interspecific competition did not significantly affect survival and individual λ at the lowest positions, indicating a predominant role for abiotic factors. Moreover, flooding duration decreased with elevation during winter (Fig. 1) and during this season we also observed a significant increase of survival at higher elevations (Fig. 3). This study therefore corroborates earlier work that identified flooding as the determining factor at species lower limits along flooding gradients (Grace & Wetzel 1981; Bertness 1991; Shipley et al. 1991; Pennings & Callaway 1992; Castillo et al. 2000; Johansson & Nilsson 2002; Lenssen et al. 2004b; Van Eck et al. 2004).

**HERBIVORY**

In addition to abiotic factors and interspecific competition, herbivory may also have contributed to the variation in fitness along our elevation gradient. In accordance with theoretical predictions (Menge & Sutherland 1976) herbivore activity increased at less disturbed positions higher on the elevation gradient. Our measure of herbivory, however, may reflect not only herbivore abundance but also changes in leaf palatability due to prevailing abiotic conditions (Louda & Rodman 1996; Rand 2002). Significant effects of herbivory were, however, never independent from elevation (Table 3), demonstrating that herbivory alone cannot explain fitness variation along the gradient. Losses inflicted on *R. palustris* merely reinforced the prevailing abiotic stress and, remarkably, even appeared to enhance survival of *Rumex crispus* seedlings with neighbours. It is possible that the reduced leaf area as a consequence of grazing also reduced water losses during dry periods (Goldberg & Novoplansky 1997), but our results suggest no more than an auxiliary role for herbivory.

**SPECIES SEGREATION OF UPPER LIMITS**

We found that upper limits of both species correspond with their relative competitive ability, supporting our second hypothesis. In non-manipulated field conditions *R. palustris* was constrained to lower positions than *R. crispus* (Fig. 1) and, accordingly, *R. palustris* was most reduced by competition with respect to all measured fitness components, i.e. survival, days until flowering and individual λ. While this accords with hypotheses assigning a dominant role to competition in determining upper limits (Grace 1990; Keddy 1990; Crawford 1992), the results also match the prediction that the weakest competitors will be more displaced from their physiological optimum (Austin 1990), particularly because both *Rumex* species had similar optima without neighbours.

Rather than being associated with a higher flooding tolerance the advantage of the weak competitor *R. palustris* at lower positions appeared to be due to more strongly developed ruderal traits, such as a relatively short life span and a high seed output (Silvertown et al. 1993). These traits may be favourable at the lowest elevations of floodplains, because regular disturbance
Conclusions

We experimentally examined the relative impact of competition and abiotic limitations along a freshwater flooding gradient, where community biomass indicated a gradual change from harsh to favourable conditions with increasing elevation. Negative neighbour effects predominated along the entire gradient although other studies have indicated that facilitation may become more important at the most stressful ends of environmental gradients (Bertness & Leonard 1997; Callaway et al. 2002). In addition to competition, there were clear abiotic limitations at both ends of this gradient, probably because our flood-tolerant Rumex species were more susceptible to drought than less tolerant species. Hence, our study provides experimental support for earlier suggestions that lower and upper ranges of species niches are determined by water excess and water deficit, respectively (Silvertown et al. 1999). This indicates that spatial variability in water availability may be an important factor promoting species richness in plant communities.

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