Explaining hydrological niches: the decisive role of below-ground competition in two closely related *Senecio* species

Maik Bartelheimer[1]*, **David Gowing**[2] **and Jonathan Silvertown**[2]

[1]*Institute of Botany, University of Regensburg, D-93040 Regensburg, Germany; and* [2]*Department of Life Sciences, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK*

Summary

1. Evidence from plant-community structure suggests that niche segregation between plant species is widespread, but the mechanisms are still generally obscure. We used experimental mesocosms to investigate the role of above- and below-ground competition in defining the distinct niche distributions of two *Senecio* species that separate along a water-table gradient in meadow habitats. In a target-border design, *Senecio* target plants were surrounded by six fence-sitting plants of *Phleum pratense* and fully factorial, randomised treatments for above-ground and below-ground competition, water level and nitrogen were applied.

2. Below-ground competition was found to be the most influential factor for plant biomass and seed production, whereas above-ground competition had negligible effects. Judging from their performances under different combinations of water level and nitrogen fertilization, the *Senecio* species showed different types of niche differentiation. *Senecio aquaticus* showed a preference for water-logged over dry soils irrespective of the presence or absence of competition. *Senecio jacobaea* showed no preference for any hydrological condition, as long as below-ground interaction was prevented. In the presence of competing roots, it showed the expected preference for dry soils, especially under N-fertilized conditions.

3. Below-ground competition was especially intense under conditions of high supply of edaphic resources and even had the potential to entirely abolish any positive effects of increased water- or nitrogen-supply. This supports the highly debated view that the importance of below-ground competition increases rather than decreases with below-ground resource supply. A functional mechanism for the dry-habitat niche of *S. jacobaea* is suggested by the severe effect of competition on this species in waterlogged soil, especially when nitrogen was added. Since such conditions favoured growth of competing neighbours, the intensified depletion of other soil resources may have been the cause of the poor performance by *S. jacobaea*.

4. *Synthesis.* Niche differentiation can either be a genetically fixed preference or a result of current competition. Below-ground competition was found to be a much stronger driver of niche differentiation than generally assumed. Even in highly productive systems it can be the principal type of interaction, which is contrary to common assumptions and which might be the case when some but not all edaphic resources are in ample supply.

Key-words: drought stress, fence-sitters, gradient, hypoxia, interspecific competition, meso-cosm, niche differentiation, *Phleum pratense*, *Senecio aquaticus*, *Senecio jacobaea*

Introduction

Spatial segregation of plant species along gradients of environmental factors is commonly observed and has been described, e.g. for hydrological gradients (Silvertown *et al.* 1999) or for

salinity gradients (Mullan Crain *et al.* 2004). However, when grown in monoculture, the majority of plant species have similar optima in regards to gradients of environmental factors or resources. Overlap between different species' so-called physiological optima (Ellenberg 1953) is found for various factors including water, temperature and pH (Ellenberg 1958). Interspecific competition often causes distributions to contract or to be displaced along a gradient from a physiological optimum

*Correspondence author. E-mail: maik.bartelheimer@biologie.uni-regensburg.de

(or fundamental niche) to an ecological optimum (or realized niche) (Ellenberg 1953). The type of niche differentiation, where a shift from the fundamental to the realized niche is caused by competition will in the following be termed 'Ellenberg-type differentiation'. As a result of niche differentiation, interacting species may become arranged in zones along a gradient. This can result in groups of species that actually coexist in an intimate interactive assemblage and species that occupy distinct (micro)habitats. Accordingly, the terms α-niche (for closely coexisting species) and β-niche (habitat niche, interaction occurs mostly with third species) are distinguished (Pickett & Bazzaz 1978; Silvertown, Dodd & Gowing 2005).

In terms of the resource-ratio-hypothesis (Tilman 1982), species are expected to dominate the zone where they have the lowest requirement (R*) for the limiting resource. An expectation derived from this hypothesis is the still much-disputed notion that the competitive ability of species should change with environmental conditions and be a relative value depending on the set of interacting species present (Mueller-Dombois & Ellenberg 1974; Pickett & Bazzaz 1978; Fargione & Tilman 2005; Fynn, Morris & Kirkman 2005, but see Keddy, Gaudet & Fraser 2000; Keddy *et al.* 2002).

The well-documented example of species segregation along hydrological gradients (Silvertown *et al.* 1999) lends itself to the investigation of functional mechanisms in niche differentiation. The hydrology of soils in many temperate meadows like floodplain meadows is governed by the relative position above groundwater and therefore the soils range from frequently dry to constantly waterlogged (e.g. Youngs, Leeds-Harrison & Chapman 1989). Water levels can have important implications for plant performance. Drought, on the one hand, is a resource stress and can result in a reduction of transpiration, photosynthesis and growth, and in damage from photoinhibition (Lawlor & Cornic 2002). Waterlogging, on the other hand, is a non-resource stress and leads to reduced O_2 diffusion (Blom & Voesenek 1996; Barber *et al.* 2004) and, consequently, to the accumulation of potentially toxic compounds such as H_2S, Mn^{2+} or Fe^{2+} (Crawford 1989). Additional factors like the availability mineral nutrients or the relative impact of above- and below-ground interactions (AI and BI, respectively) can potentially interact with water levels to play a role in niche differentiation. Levels of mineral nitrogen for instance are strongly influenced by humidity and aeration of soils (Sleutel *et al.* 2008). Levels of edaphic resources, such as water and nutrients, are also often assumed to influence or shift the relative impact of AI and BI (e.g. Grime 1973; Tilman 1982). Above- and below-ground competitions are concerned with entirely different sets of resources (Goldberg 1990) and should therefore be treated as separate factors.

Even though competition is of essential importance for niche differentiation, its mechanistic basis is not understood (Silvertown 2004), neither for α-niches nor for β-niches. Experiments that simultaneously demonstrate niche differentiation and deliver details on the mechanistic role of competition are lacking. In this study, we used two species of *Senecio* that occupy distinct β-niches along hydrological gradients to answer the following questions: (i) Does Ellenberg-type niche differentiation apply to the species? (ii) What are the relative roles of above- and below-ground competition in defining niches? (iii) Can these relative roles be influenced by varying the supply of other resources like mineral nitrogen? Following the precedent set by Ellenberg (1953), we used lysimeters (or 'mesocosms') filled with soil to regulate the water supply and impose experimental treatments, although these were of a different design and much greater in number than Ellenberg's originals. Mesocosms provide an effective compromise between laboratory experiments, where environmental control is high, but naturalism low, and field experiments, where naturalism is high but control over environmental conditions low. The point is not to mimic field conditions precisely, but to manipulate the factors of greatest interest within naturalistic limits.

Materials and methods

EXPERIMENTAL STRATEGY

A controlled outdoor experiment over two growing seasons was set-up to investigate differences in the response of the two biennial species *Senecio aquaticus* Hill and *Senecio jacobaea* L. to competition from *Phleum pratense* L. The basic experimental unit was a mesocosm (see below) that allowed the variation of water-table depths, mineral nutrition, and BI and AI. In 96 mesocosms, a balanced factorial design was set-up, with two water levels (waterlogging/drought), two nitrogen fertilizer treatments (with/without), two focal species (*S. aquaticus*/*S. jacobaea*), two treatments concerning BI (allowed/prevented) and two treatments concerning AI (allowed/prevented). Treatments were replicated three times and data were analysed by factorial analyses of variance. With five factors varied in total, this study aimed at identifying the different impacts of single factors on plant performance as well as two- or three-way interactions of factors, whereas higher order interactions were not the primary goal. In detail, *a priori* theses for the multifactorial ANOVA were that: (i) if differentiation of hydrological niches existed in the two species, it would show in a significant interaction term for the factor combination 'species' × 'water level'; (ii) if niche differentiation was caused by competitive interactions, then either of the factors 'AI' or 'BI', or both, would have a significant impact as single factors and/or significantly interact with other factors like 'target species' or 'water level'. To show unambiguously the role of plant interaction in niche differentiation would require a significant three-way interaction term of either AI or BI with the factors 'water level' and 'species'; (iii) if the impacts of AI or BI were influenced by the supply of mineral nitrogen, this would show in significant two-way interaction terms of the factors 'AI' or 'BI' with the factor 'N-fertilization'.

MESOCOSM DESIGN

We used a mesocosm-system that has been fully described by Araya (2005). Briefly, it was situated on a field site at the Open University in Milton Keynes (Buckinghamshire, UK) and comprised 96 polyvinyl chloride cylinders (mesocosms), 550 mm high and 360 mm in diameter, arranged in a randomized block design, where six rows of 16 mesocosms formed the blocks. The height of the water-table in each mesocosm was regulated by connecting the mesocosm by a hose to a float chamber (Fig. 1a) placed at an appropriate height above the ground, employing a simple gravity-based siphon principle to equalize water heights in the chambers and their connected mesocosms (see
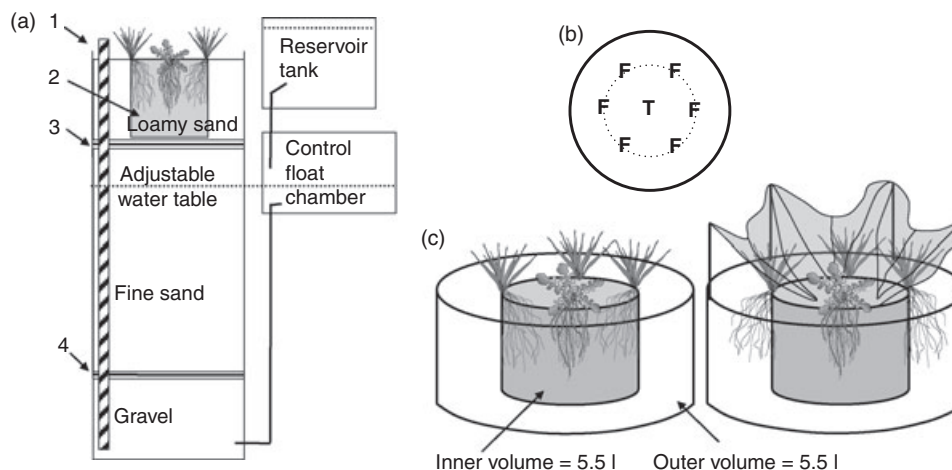
Fig. 1. Illustrations of experimental design. (a) Schematic construction plan of a mesocosm including reservoir tank and control float chamber with 1. dipwell; 2. root exclusion fabric separating inner and outer rooting volume; 3. and 4. weed block fabric. (b) Sketch of the applied hexagonal target-border design with T: target plant (either *Senecio aquaticus* or *Senecio jacobaea*), F: fence-sitting border plant *(Phleum pratense)*. (c) Two of four combinations of the planted manipulative target-border design. Left: hexagonal arrangement consisting of one target plant and six fence-sitting neighbours with both shoot interaction allowed (no netting) and root interaction allowed (fence sitter roots in the inner volume). Right: control treatment with both shoot interaction prevented (netting) and root interaction prevented (fence sitter roots in the outer volume).

Snow & Tingey 1985). The float chambers were 18 L containers that were constantly refilled with water from the reservoir tank to balance evapotranspiration losses. When precipitation exceeded evaporation, water flowed from the mesocosms to the float chambers and escaped via overflow drainage holes (Araya 2005).

The bottom part of the mesocosm, to a level just above the inlet hose connection (100 mm), was filled with coarse gravel (average diameter 10 mm). Weed block fabric was used to separate the gravel from an overlying 300 mm layer of fine sand. On top of the sand lay 110 mm of rooting medium [loamy sand with three parts silica sand (WBB Minerals, Sandbach, UK) and two parts of loam (supplied by Woburn Experimental Farm, Buckinghamshire, UK)]. Root penetration by plants beyond this medium was effectively prevented using weed block fabric. Where the weed block and the root exclusion fabric (see below) had direct contact, hydraulic conductivity was assured by a thin layer of fine sand between the fabrics.

Two different water levels were used in this experiment: for the waterlogging treatment, water levels were set to 70 mm below the soil surface. For the drought treatment, water was allowed to drain freely. Water levels or effective drainage were controlled on a regular basis. To prevent frost damage to the system, the mesocosms were drained during the colder winter months of January through March 2007.

METEOROLOGICAL CONDITIONS

General climatic conditions in Milton Keynes (UK), where the experiment was situated, are temperate and relatively oceanic. At the close-

by Woburn Meteorological Station, the mean temperature over the course of the experiment was 10.7 °C. The 2006 vegetation period saw a mean temperature of 14.7 °C with a maximum value of 34.6 °C and a minimum of −3.8 °C (Table 1). Mean daily precipitation during the 2006 vegetation period was 1.9 mm. The 2007 vegetation period saw moderate temperatures (mean 13.6 °C, maximum 27.8 °C), a mean daily precipitation of 2.0 mm and one extended period with sparse precipitation (36 days).

SPECIES DESCRIPTION AND COMPETITION TREATMENTS

Senecio jacobaea and *S. aquaticus* are two closely related Asteraceae species with distinctly different occurrence concerning soil moisture (Kirk, Vrieling & Klinkhamer 2005). *Senecio jacobaea* occurs on comparatively dry soils of temperate grasslands (sand dunes, some open woodland, waste land, waysides and neglected or overgrazed pastures), while *S. aquaticus* occurs on the wet soils of marshes, wet meadows and ditches (Clapham, Tutin & Moore 1987; Kirk, Vrieling & Klinkhamer 2005). The range of *S. jacobaea* covers Europe to 66° N, the Caucasus and Western Asia. *Senecio jacobaea* has been introduced to New Zealand, Australia, South Africa and North and South America (Clapham, Tutin & Moore 1987). The range of *S. aquaticus* covers Western and Central Europe from Northern Italy to 63° N, and eastwards to Posen and lower Silesia (Clapham, Tutin & Moore 1987). The species often co-occur in the same habitat (Webb & Scannell 1983), while their micro-habitats are distinct, as is illus-

Table 1. Meteorological data over the duration of the experiment. Source: Woburn Meteorological Station, Buckinghamshire, UK

	Period		
Meteorological parameter	April 2006–October 2006	November 2006–March 2007	April 2007–August 2007
Minimum temperature (°C)	−3.8	−8.2	−1.4
Maximum temperature (°C)	34.6	16.7	27.8
Mean daily precipitation (mm)	1.93	1.75	2.04
3 longest periods with precipitation < 2 mm day^{-1} (days)	17; 16; 14	19; 15; 15	36; 18; 15

trated by an example reported by Kirk, Vrieling & Klinkhamer (2005): in the Zwanenwater Reserve in the Netherlands *S. jacobaea* occurs on the dryer soil of sand dunes, *S. aquaticus* on a lake fringe and their hybrid on the intermediately humid soil in-between. Between these two focal species, *S. aquaticus* is far more specialized with respect to hydrological conditions, since it occurs on water-logged soils. Some features known to facilitate its growth under such conditions are an extensive aerenchyma (Smirnoff & Crawford 1983), the ability of roots to adapt their metabolism (Albrecht, Biemelt & Baumgartner 1997) or partly even to sustain a balanced metabolism in hypoxic soil (Biemelt, Albrecht & Wiedenroth 1996).

Phleum pratense is a grass with a much more general distribution with respect to soil moisture and occurs in all grasslands of the northern temperate regions except for moorland and higher mountains (Clapham, Tutin & Moore 1987). It often co-occurs with *S. jacobaea* (e.g. in Cynosurion) (Dierschke 1994) and occasionally with *S. aquaticus*, e.g. in associations of Bromo-Senecionetum aquatici (Ellenberg 1996). It is also a species known to be comparatively insensitive to hypoxic stress (Bertrand *et al.* 2001).

We used a manipulative target–border design (see Fig. 1b) where one of the two *Senecio* species was always used as the target and was surrounded by six border plants of *P. pratense*. Four combinations of the factors above-ground competition and below-ground competition were implemented (see Fig. 1c): competition above- and below-ground, root competition prevented with fine nylon mesh, shoot competition prevented with nettings, root and shoot competition prevented (control). To avoid typical shortcomings of exclusion tubes (reduced rooting space, limited movement of soil resources), we applied a novel fence-sitter approach (following from Maina, Brown & Gersani 2002; O'Brien, Gersani & Brown 2005). It is based on a division of the rooting medium into an inner and an outer volume, both containing 5.5 L. The inner volume is cylindrical in shape (diameter 25 cm, height 11 cm) and enclosed by a 52 μm nylon mesh (Plastok Associates Ltd., Birkenhead, UK) that plant roots cannot penetrate. Border plants are always present as fence sitters, but they can be rooted either in the inner volume, allowing BI with the target plant, or they are rooted in the outer volume, with no BI possible. This keeps constant the rooting space of the target as well as the border plants, and it allows the movement of the soil solution. Only the presence/absence of competing roots is varied (Fig. 1c). The intention of this design is to minimize any impact on the border plants that might result from their position relative to the exclusion fabric.

Similarly, AI is prevented or allowed by the presence/absence of nylon netting (2 cm mesh), which was fixed with bamboo sticks to keep the border plants separated from the target. New leaves of border plants were rearranged under the netting on a regular basis. Border plants without netting were handled in a similar manner to avoid unintended effects (Cahill, Castelli & Casper 2002). Once a year in mid-July, flowering stalks of *P. pratense* were cut 10 cm above the ground. The aim was to simulate the yearly mowing that is the most common grassland management in English meadows. However, in the second year *Senecio* plants were left uncut to prevent disruption of seed production shortly before harvest.

PLANT CULTURE

Seeds were collected from field sites (*S. aquaticus*: West Sedgemoor, Somerset, UK) or supplied by Botanical gardens (*S. jacobaea*: Botanical Garden Göttingen, Germany; *P. pratense*: Botanical Garden Hohenheim, Germany), sown in early spring 2006, pricked and raised in a glasshouse and hardened under ambient conditions close to the mesocosms for some weeks. Planting took place in mid-May 2006,

when plants were prepared as follows: for *P. pratense* only plants with five tillers were selected and roots were pruned to a length of 4 cm. Mean total biomass (mean ± SE for $n = 8$), measured on representative plants, was 0.377 ± 0.043 g dry wt. For *S. aquaticus* and *S. jacobaea*, only plants with four leaves were chosen to assure similar sizes both within and between the two species, and roots were pruned to a length of 4 cm. Mean total biomasses (mean dry wt. ± SE for $n = 6$) were 0.041 ± 0.005 g for *S. aquaticus* and 0.030 ± 0.005 g for *S. jacobaea* and were not significantly different (Student's *t*-test).

FERTILIZER TREATMENT AND NUTRIENT CONTENTS

Fertilizer treatment started in July 2006, when all plants were established, and was carried out weekly throughout the growing season (2006: until October; 2007: from April until harvest in August). A small watering can was used to evenly distribute 0.2 g NH_4NO_3 dissolved in 200 mL tap water over the soil surface of the fertilized treatments. The unfertilized treatments received tap water only. Yearly amounts added up to a total of 0.63 g N mesocosm^{-1} in 2006 and 1.26 g N mesocosm^{-1} in 2007, respectively. With a soil surface of 0.1 m^2 mesocosm^{-1}, this rate corresponded to 63 kg N ha^{-1} year^{-1} (in 2006) and 126 kg N ha^{-1} year^{-1} (in 2007) and matched values recommended to avoid N-limitations in agricultural systems (Neeteson 1990).

Bicarbonate-extractable P (mean ± SD for $n = 4$: 10.51 ± 1.11 mg kg^{-1}) lay within the range of rather P-poor soils (Marschner 1997). K$^+$ availability (calcium-acetate-lactate-extracted) was generally low as well (compare Hoffmann 1991): a comparison between N-fertilized and non-fertilized soils (sampled in spring of the second growing season and both comprising a balanced set of waterlogged and dry treatments) revealed values of 7.63 ± 1.54 mg kg^{-1} for unfertilized soils and 6.23 ± 0.68 mg kg^{-1} in N-fertilized soils (mean ± SD for $n = 12$; $P < 0.01$ in *t*-test).

SEED COLLECTION AND PLANT HARVEST

Seeds production in *Senecio*-plants occurred in the second year of the experiment during a period from early June to harvest in August. They were collected whenever the drying of the according flower heads indicated seed ripening. Seeds were air-dried, cleaned from pappae by means of a 1 mm sieve and weighed.

The final and destructive plant harvest took place during the last week in August of the second year, when several plants started monocarpic senescence. Roots were washed out from the root balls by a gentle water spray. Intermingled root systems were divided in a water basin and distinguished by their connection to the stem, their colour and morphology. All plant parts were oven-dried at 80 °C for 3 days and weighed.

DATA ANALYSIS

To quantify competition intensity we used the log Response Ratio (lnRR; Goldberg *et al.* 1999) with:

$$lnRR = ln(DW_{control}/DW_{interaction})$$

where $DW_{control}$ is the mean total dry weight of the target plants grown with all interaction prevented (control) and $DW_{interaction}$ is the total dry weight of a single target plant grown in the presence of AI and/or BI. Since the formula's numerator is a mean value and the denominator is an individual value, it is possible to calculate the lnRR for the control plants and thus to get information about their variance. This was done since it was required for the

Table 2. Results from five-way-multifactorial ANOVA performed individually for the target plant parameters total biomass, log Response Ratio (lnRR) and total seed mass. Some of the two- or more-factorial interaction terms that were not related to the defined research questions and yielded no significant results for any of the parameters were omitted for the sake of clearness (AI, above-ground interaction; BI, below-ground interaction; bold values indicate statistical significance, italic values indicate marginal significance).

Source of variation	d.f.	Total biomass			lnRR			Total seeds mass		
		SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Target species	1	8.01	12.30	**< 0.001**	0.40	0.55	0.4594	3.03	58.14	**< 0.001**
Water level	1	0.00	0.00	0.9480	4.88	6.76	**0.0119**	0.07	1.42	0.2400
AI	1	0.00	0.00	0.9900	0.00	0.00	1.0000	0.00	0.00	0.9900
BI	1	31.32	48.10	**< 0.001**	33.86	46.83	**< 0.001**	1.37	26.25	**< 0.001**
N-fertilization	1	9.79	15.04	**< 0.001**	4.86	6.73	**0.0120**	1.56	29.86	**< 0.001**
Target species × water level	1	13.39	20.57	**< 0.001**	1.48	2.05	0.1580	0.15	2.87	*0.0950*
Target species × AI	1	0.02	0.03	0.8584	0.01	0.02	0.8910	0.01	0.1980	0.6580
Target species × BI	1	2.02	3.12	*0.0833*	2.40	3.31	*0.0739*	0.00	0.04	0.8404
Water level × AI	1	0.03	0.05	0.8291	0.03	0.04	0.8505	0.07	1.38	0.2450
Water level × BI	1	3.38	5.19	**0.0265**	3.51	4.86	**0.0315**	0.00	0.018	0.8937
AI × N-fertilization	1	0.22	0.33	0.5658	0.24	0.33	0.5662	0.00	0.01	0.9297
BI × N-fertilization	1	8.26	12.69	**< 0.001**	8.49	11.74	**0.0011**	0.94	18.04	**< 0.001**
Water level × AI × N-fertilization	1	0.03	0.045	0.8297	0.04	0.05	0.8215	0.01	0.18	0.6711
Water level × BI × N-fertilization	1	4.34	6.66	**0.0124**	4.79	6.62	**0.0127**	0.05	1.00	0.3202
Error	62	37.11			41.22			3.23		

Analysis of Variance outlined in Table 2. Values of lnRR are symmetrically distributed around zero and there is no ceiling to the maximum or minimum value. Positive values indicate competition, negative values indicate facilitation.

All statistical tests (factorial ANOVA in Generalized Linear Models, ANOVAs with *post hoc* Fischer LSD-tests and *t*-tests) were carried out with STATISTICA 6.0 (StatSoft, Inc., Tulsa, OK, USA). Where assumptions of normality or homogeneity of variances were not fulfilled, data were log-transformed [dry wt.: $\log_{10}(x + 0.1)$; seeds: $\log_{10}(x + 1)$]. In the case of border plant dry weight, plants from N-fertilized and non-fertilized treatments formed two distinct statistical populations and were therefore analysed separately.

Results

MULTIFACTORIAL ANALYSIS

The five-way multifactorial ANOVA (Table 2) examined the impact of single and interacting factors on plant performance as assessed by three different measures: the biomass produced after two growing seasons, the lnRR and the seeds collected during the second vegetation period. According to their high *F*-values, single factors that significantly influenced plant biomass were the presence of root interaction, N-fertilization and species identity. AI had no effect. Water level by itself had no effect on biomass, but there was a strong interaction between the factors water level and species identity. This indicates that, over the whole data set, the two species had different hydrological preferences (Table 2, Fig. 2a). Further significant interactions were found especially when the presence of below-ground competition was involved, although neither of the according *F*-values was as high as the one for BI alone.

As far as the lnRR is concerned, species identity had no significant influence (Table 2), but in contrast to the same tests on biomass (see above), water level by itself significantly influ-

enced the lnRR. There was no significant 'species' × 'water level' interaction affecting lnRR. N-addition not only had an influence on biomass (see above), but also on the intensity of competition.

As a fitness-related parameter, seed production was likewise analysed using multifactorial ANOVA statistical tests (Table 2). Results resembled those for biomass, although *F*-values indicate that the impact of BI is somewhat lessened in comparison with the multifactorial ANOVA based on biomass. Nitrogen addition had a stronger impact on seed production than on biomass.

The multifactorial ANOVA delivered three important findings: (i) the two *Senecio*-species have different hydrological preferences; (ii) there are significant interaction terms of below-ground competition with factors like water level or fertilization; (iii) below-ground competition has an unambiguously strong impact.

Since the multifactorial ANOVA merely gives information about the impact of a factor but not about whether the impact is positive or negative, the following more detailed analyses were carried out to address the three findings in more detail.

NICHE DIFFERENTIATION

(i) The species' different hydrological preference is addressed in Fig. 2. Looking at the whole biomass data set, it became clear that *S. aquaticus* grows better under waterlogged conditions, while *S. jacobaea* grows slightly, although not significantly, better under dry conditions (Fig. 2a). However, when taking into account whether plants were exposed to BI (Fig. 2c,b), it becomes clear that *S. aquaticus'* preference for waterlogged conditions was largely independent of the presence or absence of below-ground competition. By contrast, *S. jacobaea* showed no preference for any water condition
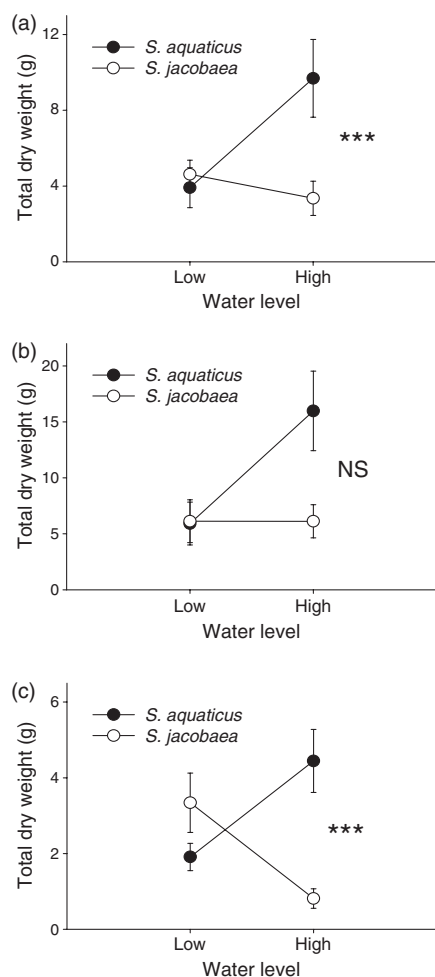
Fig. 2. Impact of different water levels on biomass production (mean ± SE) in the two target species *S. aquaticus* and *S. jacobaea* for (a) the whole data set (statistics according to Table 2, *n* = 24), (b) plants grown in the absence of below-ground interactions (statistics of two-factorial ANOVA-comparisons: SS = 3.42, d.f. = 1, *F* = 3.82, *n* = 12) and (c) plants grown in the presence of below-ground interactions (statistics of two-factorial ANOVA-comparisons: SS = 15.78, d.f. = 1, *F* = 18.62, *n* = 12). Significant interaction of the factors 'water level' and 'species' (***$P < 0.001$).

when below-ground competition was absent (Fig. 2b). Its distinct preference for drier conditions was only visible in the presence of BI (Fig. 2c).

IMPACT OF BELOW-GROUND COMPETITION

(ii) Some features of how below-ground competition impacted on biomass are illustrated by its significant interaction terms with both water level (Fig. 3a) and N-fertilization (Fig. 3b). In absence of below-ground competition both high water levels and N-fertilization resulted in increased biomass production, while there was no such increase observed in the presence of BI.

(iii) The strong impact of below-ground competition and the species' reactions to further factors can be studied in greatest detail by breaking down the biomass data set to all 32 different combinations of species and treatments (Fig. 4). Under certain combinations of water level and N-fertilization, e.g. under dry and nitrogen-poor conditions (Fig. 4a), no clear species differences and no clear reactions to competition treatments could be detected. Under waterlogged and nitrogen-poor conditions (Fig. 4b), *S. aquaticus* showed an increase in biomass. Under these conditions, there was a first tendency of lower biomass production in the presence of BI. Meanwhile, *S. jacobaea* showed no tendency of increasing biomass under waterlogging. It reacted more clearly under dry and N-fertilized conditions (Fig. 4c), where it produced more biomass than under unfertilized conditions and the negative effects of BI were starting to show. Under these conditions, the two *Senecio*-species exhibited a striking similarity as far as produced biomass and reaction to treatments is concerned (Fig. 4c). Waterlogged and N-fertilized conditions brought out the most pronounced species differences and reactions (Fig. 4d). In *S. aquaticus*, control plants and those subjected to solely AI, grew vigorously, but strongly reacted to BI. Plants of *S. jacobaea* also grew very well in waterlogged and fertilized soil, but only in the absence of BI. Under these resource-rich conditions BI reduced the biomass production in *S. jacobaea* to the lowest level in the whole data set (Fig. 4d). One especially noticeable observation is the impact of below-ground competition on plants of *S. jacobaea* under conditions of waterlogging. *Senecio jacobaea* plants that were not fertilized (Fig. 4b, grey bars in treatments B C and A + B C) grew quite well and some even produced seeds (data not shown). The corresponding plants in the N-fertilized treatment (Fig. 4d) grew considerably less than this and no seeds were produced (not shown). At the same time, all other treatments responded positively to N-fertilization (Fig. 4d).

The competitive response, calculated as the lnRR (Fig. 5) is an index that compares a competition treatment with the respective control treatment. In treatments without root interactions, lnRR values were always low, again indicating low competition. Values were considerably higher when roots had contact. In *S. jacobaea*, the most striking competitive response to below-ground competition was found under waterlogged and N-fertilized conditions, which corresponds to the above described results. Quite differently, in *S. aquaticus*, the most intense responses to below-ground competition were found under fertilized conditions, and this was irrespective of the applied water level. So this comparison pinpoints the two species' different reactions. For *S. jacobaea*, the most adverse effects were found under a combination of waterlogging and N-fertilization, for *S. aquaticus* the most adverse effects were found under N-fertilization, irrespective of water level.

BORDER PLANTS

The growth of the fence-sitting border plants sheds light upon competitive interactions under different hydrological and nutritional conditions. Total dry weight of all six plants in each mesocosm was measured (Fig. 6), including roots and shoots cut to simulate mowing. Biomass production of *P. pratense* was strongly increased by N-fertilization (Fig. 6c,d). Impor-
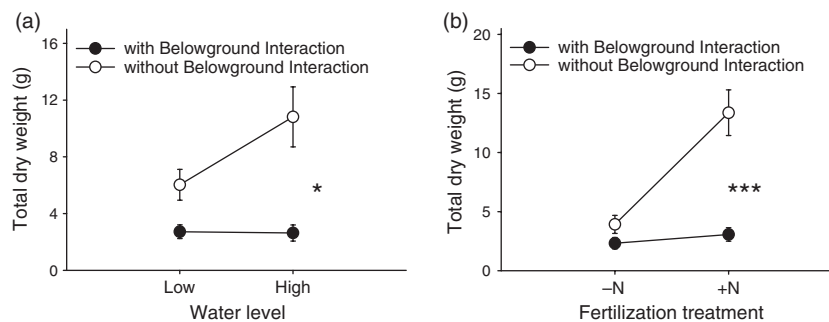
Fig. 3. Impact of the presence of below-ground interactions on biomass production in the whole data set (mean ± SE for $n = 24$, statistics after Table 1) depending on (a) the two different water levels and (b) the two nitrogen fertilization treatments. Significant interaction terms in two-factorial ANOVA-comparisons (*$P < 0.05$, ***$P < 0.001$).
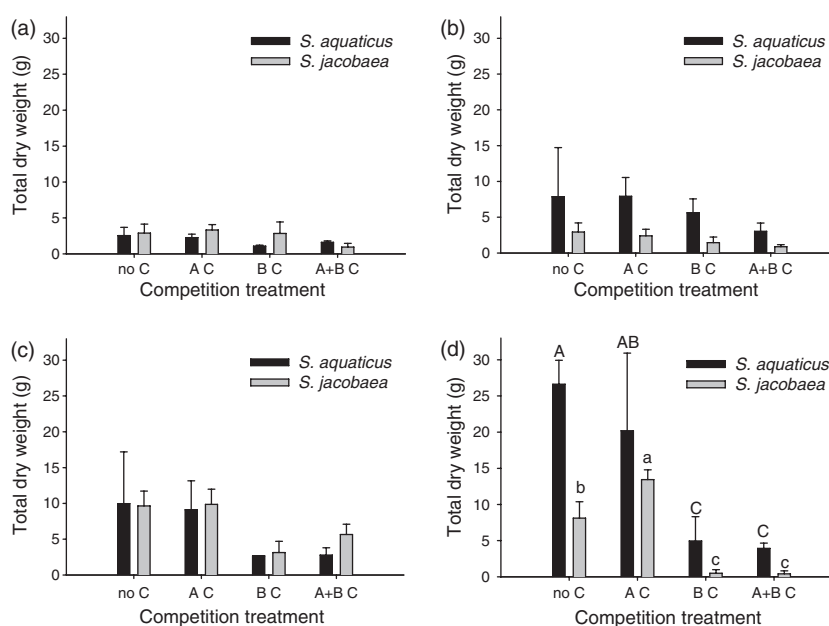

Fig. 4. Total biomass (mean ± SE for $n = 3$) of the two focal species *S. aquaticus* and *S. jacobaea* in different competition treatments under (a) dry and unfertilized conditions, (b) waterlogged and unfertilized conditions, (c) dry and N-fertilized conditions, and (d) waterlogged and N-fertilized conditions. Different capital letters indicate statistically significant differences in ANOVA comparison with *post hoc* LSD-test for *S. aquaticus*. Different lower case letters indicate statistically significant differences in ANOVA comparison with *post hoc* LSD-test for *S. jacobaea*. no C: no competition; A C: above-ground competition only; B C: below-ground competition only; A + B C: simultaneous above- and below-ground competition.

tantly, growth of *P. pratense* was by no means decreased by waterlogging. For statistical analyses N-fertilized and unfertilized plants formed two distinct statistical populations [unfertilized: 55.51 ± 2.58 g (mean DW ± SE); fertilized: 179.52 ± 7.62 g; *t*-test: $P < 0.0001$ for $n = 48$], so that the multifactorial ANOVA had to be carried out separately for both (Table 3). In the non-fertilized treatment, border plants responded to water levels with a significant increase under waterlogged conditions (Table 3, compare Fig. 6). There was also an unintended significant effect of BI (for N-fertilized border plants) and an unintended cross-effect of AI and BI (for non-fertilized plants). Summarising the growth reactions of the border plants, it can be stated that the high resource supply in waterlogging and especially under N-fertilization increased their growth.

Discussion

Although niche differentiation may have a central role in structuring and defining plant communities, studies that examine the functional mechanisms underlying niche differentiation are scarce. A number of studies demonstrate the role of competition for niche segregation, for example in salt marshes (Bertness 1991; Pennings & Callaway 1992), in grasslands with gradients in either nitrogen (McGraw & Chapin 1989), or in disturbance and nutrients (Turkington, Klein & Chanway 1993), or in moisture (Barnes 1985). Among these, only three studies relate the species' ecological preferences to differences in physiology or morphology, namely the ability to oxygenate the soil in marsh systems (Bertness 1991), the ability to efficiently take up or use nitrogen in a nitrogen gradient (McGraw
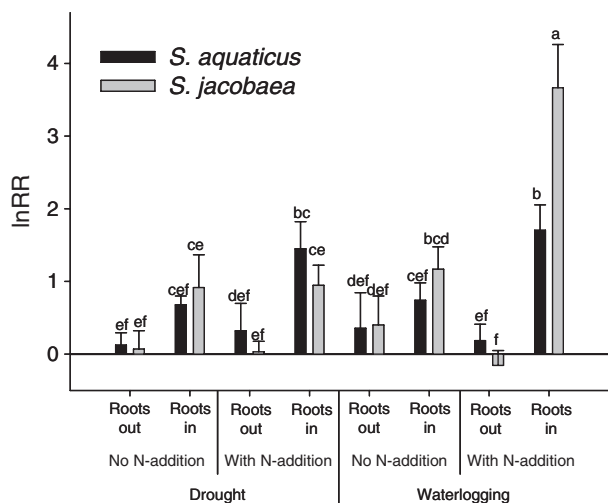
Fig. 5. Competitive response of the two *Senecio*-species to different treatment combinations calculated as log Response Ratio (mean ± SE for *n* = 6). Different lower case letters indicate statistically significant differences in ANOVA comparison (*F* = 8.09, d.f. = 15, *P* < 0.001) with *post hoc* LSD-test. Because of the negligible effect of above-ground interactions, all treatments with or without above-ground netting were pooled.

& Chapin 1989), or to different abilities to control water loss in moisture gradients (Barnes 1985).

The functional details revealed by our study show that (i) two different types of niche differentiation occurred, (ii) below-ground competition can be a much stronger driver of niche differentiation than commonly assumed and (iii) that it can be

especially strong under conditions of high supply of below-ground resources.

TWO TYPES OF NICHE DIFFERENTIATION

Since Ellenberg's (1953) pioneering experiments, it has been clear that niche differentiation is driven by competitive interactions which reduce the overlap between species in the realised niches, compared with their physiologically determined fundamental niches. However, this seems to be only half the story. First, in *S. jacobaea*, we found a prime example for Ellenberg's mechanism of niche differentiation. Without below-ground competition, *S. jacobaea* showed no preference for either dry or wet soil conditions (Fig. 2b). However, in the presence of competing roots, *S. jacobaea* produced a three times smaller biomass than in waterlogged conditions (Fig. 2c). Secondly, in *S. aquaticus*, we also found niche differentiation: the species showed a clear preference for waterlogged over dry soils (Fig. 2). But in contrast to *S. jacobaea* and to Ellenberg-type differentiation, this preference existed irrespective of the presence of competition (Fig. 2b,c). Competition merely accentuated this preference (Fig. 2c). One has to keep in mind that such a preference can be seen as a result of past evolution under competition (Connell 1980).

With *S. jacobaea* being the more generalist species and *S. aquaticus* the more specialised species [considering its relatively restricted distribution over Europe, its occurrence in only relatively few habitat types and its outstanding ability to increase the porosity of its aerenchyma (Smirnoff & Crawford 1983; Justin & Armstrong 1987)], a thesis would be that
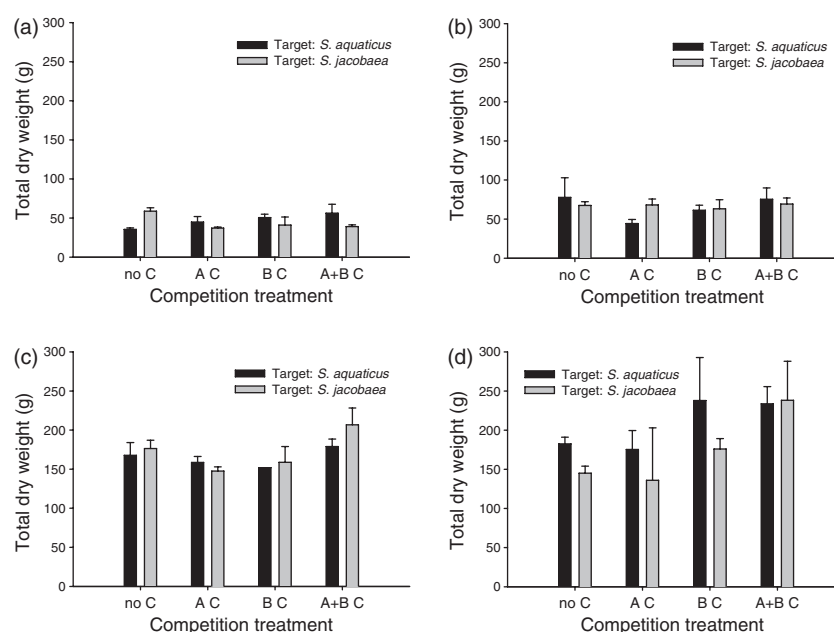
Fig. 6. Total biomass (mean ± SE for *n* = 3) of the six *P. pratense*-plants surrounding either *S. aquaticus* or *S. jacobaea* in different competition treatments under (a) dry and unfertilized conditions, (b) waterlogged and unfertilized conditions, (c) dry and N-fertilized conditions, and (d) waterlogged and N-fertilized conditions. ANOVA comparisons within species yielded no significant differences among competition treatments under any set of water- and fertilizer conditions. no C: no competition; A C: above-ground competition only; B C: below-ground competition only; A + B C: simultaneous above- and below-ground competition.

Ellenberg-type differentiation applies mainly to generalist species, while genetically fixed niches are mainly found in specialised species. Support comes from a result from Ellenberg's groundwater trials themselves, where both the physiological and ecological optimum of the wet-tolerant species *Poa palustris* were found in relatively high groundwater levels (Ellenberg 1953).

This hypothesis applies to the habitat-niche (or β-niche) rather than the α-niche (following Pickett & Bazzaz 1978), since this is what this paper examines: hydrological conditions of the micro-habitats of *S. aquaticus* and *S. jacobaea* are quite distinct. Kirk, Vrieling & Klinkhamer (2005) describe a typical case of the species' occurrence where *S. aquaticus* occurs at a lake fringe, *S. jacobaea* on dryer dunes (about 100 m apart) and their hybrid in-between.

BELOW-GROUND COMPETITION AS A DRIVER OF HYDROLOGICAL NICHE DIFFERENTIATION

We found that BI had a striking impact in this experiment. Among all examined factors, it had the strongest influence on the production of biomass and on the intensity of competition calculated as the lnRR. It had a highly significant influence on the production of seeds, too (Table 2). This is rather unexpected, since below-ground resource-sharing is generally regarded as less antagonistic than above-ground competition (e.g. Weiner 1986; Casper & Jackson 1997; Bartelheimer, Steinlein & Beyschlag 2008).

When below-ground competition was present, the otherwise positive effects of high water availability (Fig. 3a) and high nitrogen availability (Fig. 3b) were levelled. Most probably, this was caused by the vigorous growth of competitors that profited from these conditions (compare Table 3 and Fig. 6). In fact, *P. pratense* generally grew better under fertilized conditions and also under waterlogged conditions as compared with dry conditions (Table 3).

Consistently, the more detailed analyses on effects of different treatments (Figs 4 and 5) revealed that *S. jacobaea* suffered from below-ground competition under all varied combinations of water level and N-fertilization, but by far to the strongest extend under waterlogged and N-fertilized conditions. Some treatments were even observed, where, all else

equal, fertilized plants grew less than unfertilized plants, most probably because of increased below-ground competition. The mechanism here is thus that interacting species profit differentially from resource increase. The species that profits less suffers from increased competition by its boosted neighbours (Fig. 6). This could well reflect mechanisms in natural systems. Contested resources appear to be water and/or nitrogen (Fig. 4), but since below-ground competition is still severe when these are in ample supply, macronutrients like P or K suggest themselves. It is also tempting to hypothesise that the presence of neighbour roots reduced the oxygen availability to a level too low for species with a low tolerance to anoxia.

PRODUCTIVITY AND THE INTENSITY OF BELOW- AND ABOVE-GROUND COMPETITION

Even though this experiment was not primarily intended to contribute to the Grime-Tilman-debate, our data allow a statement on the inter-relation between productivity and the intensity of above- and below-ground competition.

According to Grime's theory (e.g. Grime 1973), the importance of both above- and below-ground competition should increase with productivity. On the other hand, according to Tilman (e.g. Tilman 1988) the intensity of below-ground competition should decrease with productivity and the intensity of above-ground competition increase.

Although the intensity of competition does not necessarily equal its importance (Brooker & Kikvidze 2008; Lamb, Kembel & Cahill 2009) a high intensity of competition is certainly a pre-condition for it to be important. It is therefore interesting to see that (i) highest intensities of below-ground competition were found in N-fertilized and waterlogged treatments (Fig. 5), i.e. under conditions of highest productivity (compare Fig. 4d) and (ii) above-ground competition, with its low intensity throughout the experiment (Table 2), did not increase or decrease with productivity. The first result would be quite close to Grime's predictions (see above), but not the second. One likely reason why above-ground competition did not increase with productivity is that with the high supply of two otherwise limiting edaphic resources (water and N) a third edaphic resource became limiting (von Liebig 1840; Davidson &

Table 3. Results from four-way-multifactorial ANOVA for total biomass of border plants performed individually for non-fertilized or N-fertilized conditions. Two- or more-factorial interaction terms that yielded no significant results for either of the parameters were omitted for the sake of clearness (AI, above-ground interaction; BI, below-ground interaction; bold values indicate statistical significance, italic values indicate marginal significance)

Source of variation	d.f.	Total biomass without N-fertilization			Total biomass with N-fertilization		
		SS	F	P	SS	F	P
Target species	1	7	0.03	0.8601	6345	2.70	0.1101
Water level	1	4722	21.72	**< 0.001**	1359	0.58	0.4524
AI	1	116	0.53	0.4705	1729	0.74	0.3973
BI	1	63	0.29	0.5941	13530	5.76	**0.0224**
AI × BI	1	982	4.52	**0.0414**	7520	3.20	*0.0831*
Error	32	6956			75185		

Howarth 2007; Elser *et al.* 2007). We suggest that a productivity-induced transition to above-ground competition as predicted by both Grime and Tilman will only occur once all essential edaphic resources are in ample supply.

USE OF MESOCOSMS TO IMITATE NATURAL CONDITIONS

If we want to draw conclusions from our experiment that have relevance for the natural situation, we have to make sure that experimental conditions match those outside. As far as the factors soil and availability of nitrogen, water levels, and management (mowing) are concerned, we are confident that natural conditions of the two *Senecio*-species were matched as far as possible.

What is inevitably artificial in such experiments is the limitation of rooting space, which can result in an overestimation of the influence of below-ground competition (McConnaughay & Bazzaz 1992; Bartelheimer, Steinlein & Beyschlag 2006). The mesocosms design did not allow roots to go deeper than 11 cm, but in the case of meadows, this is not far from the natural situation. Schenk & Jackson (2002) examined an extensive data base of rooting depths in different systems and found temperate meadows to be the most shallowly rooted ecosystem examined. 50% of all roots were contained in the upper 5 cm of soil and about 85% in the upper 10 cm. As far as wet soils are concerned, the aeration status very rapidly decreases with soil depth (Barber *et al.* 2004). And in drier meadows, maximal nutrient contents are usually found in the more humose layers of the upper centimetres (Schenk 2004).

A second topic to be addressed is plant density, especially during the establishment of plants. Our method of planting seedlings into bare soil is clearly different from germination and establishment processes in natural meadows, where seeds usually germinate after hay cutting or in gaps of established vegetation. We cannot claim that our results account for interactions during natural establishment, where for example AI could be important factors. But since we chose biennial (rather than perennial) species and examined them for 2 years, we are confident that our results as a whole are applicable for more general scores.

Conclusions

We could demonstrate that next to Ellenberg-type niche differentiation, we have to consider there might be cases of genetically fixed niche preference in meadow species. Below-ground competition can be a strong driver of niche differentiation and can be much stronger than generally assumed. Even in highly productive systems it can be the principal type of interaction, which is contrary to common assumptions and which might be the case when some but not all edaphic resources are in ample supply. Finally, as a suggestion requiring further investigation, we suggest that soil oxygen can be a resource that can be contested by plants and that can result in the competitive exclusion in waterlogged habitats.

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