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Competition components along productivity gradients – revisiting a classic dispute in ecology

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Competition is ubiquitous in plant communities with various effects on plant fitness and community structure. A long-standing debate about different approaches to explain competition is the controversy between David Tilman and Philip Grime. Grime stated that the importance of competition relative to the impact of the environment increases along a productivity gradient, while Tilman argued that the intensity of competition is independent of productivity. To revisit this controversy, we assumed that the effects of plant–plant interactions are additive and applied the new competition indices by Díaz-Sierra et al. (2017) in a field experiment along a productivity gradient in S-Germany, using the rare arable plant *Arnoseris minima* as a study species. The 'target technique' was applied, to separate the effects of root and shoot competition. The study plants were exposed to five competition treatments with three replicates in 18 sites, respectively. We investigated the expectation that root competition is more intense in unproductive sites than shoot competition. Additionally, we predicted survival to be less affected by competition than growth-related plant parameters. Using the biomass of individuals without competition as a proxy for site productivity there was a positive relationship with competition importance but no relationship with competition intensity when plants experienced full competition. Survival of the target plants was unaffected by competition. Root competition was the main mechanism determining the performance of the target plants, whereas the effect of shoot competition was relatively low albeit increasing with productivity. We conclude that when considering plant–plant interactions additive both Grime's and Tilman's theories can be supported.

Keywords: competition importance, competition index, competition intensity, rare arable plant, root competition, shoot competition

Introduction

Competition is a common phenomenon in plant communities with well-known effects on plant fitness and community structure (Aschehoug et al. 2016). Thus, the significance of competition was already described by Darwin (1859), and empirical studies on this phenomenon date back to the rise of modern ecology (Clements 1929). Since then, various experimental and modelling approaches have been performed to better understand the patterns and mechanisms of plant competition, among them some classic controversies between contrasting theories and the scientists behind them (Grace 1990). Most prominent was the debate between David Tilman and Philip Grime starting in the 1980s. Nowadays, many ecologists would define competition as 'the process by which two or more individuals acquire resources from a potentially common, limiting supply' (Craine et al. 2013). The main resources plants compete for are water, nutrients and light.

Competition experiments have often been conducted along environmental gradients that control productivity, and the theories of both Grime (1979) or Tilman (1982) were advocated to explain the results of such experiments. Grime's (1979) approach is called the *life history trade-off theory* which is an expansion of the r- and K-selection theory by MacArthur and Wilson (1967) where plants differ in their adaptation to stress and disturbance. Therefore, plants are considered 'competitive' when they are adapted to low levels of stress and low levels of disturbance, and 'stress-tolerant' when tolerating high levels of stress and low levels of disturbance, whereas species adapted to high disturbance and low stress are called 'ruderals'. In his model the plant that is most successful in capturing resources is the superior competitor. Grime (1979) further presumed an evolutionary tradeoff for plant traits, giving plants either the ability to tolerate stress or to grow rapidly. Unproductive environments are, therefore, inhabited by stress-tolerant species which per definition are not good at capturing resources. Competition is hence only of minor importance in these habitats relative to other environmental stress factors.

Tilman's (19820 *resource ratio theory*, on the other hand, is based on a quantitative mechanistic model. Its main assumption is that plants reduce resource concentrations down to a species-specific level called R* by taking up nutrients or water or by shading other plants; below this level plants are unable to survive. When two species compete for the same resource the one with the lower R* will eventually outcompete the other species. This theory further assumes that in unproductive habitats competition acts mainly below-ground since, the above-ground biomass is not sufficient to reduce light effectively, while productive habitats will develop a dense canopy so that competition is mainly above-ground, i.e. for light. Tilman (1982) considered that there are evolutionary tradeoffs in plants regarding their competitive ability at different ratios of light to soil resource. Therefore, a plant can either be a good competitor for light by allocating large proportions of its resources to stems and leaves, or a good competitor for soil resources by allocating more resources to roots. Thus, competition is intense at all levels of productivity, while the resource for which plants compete shifts from nutrients and water at low productivity to light at high productivity.

To test the theories of Grime and Tilman, ecologists developed various indices for competition, where competition intensity 'is a reduction in the growth of species A as a consequence of the presence of species B' (Brooker et al. 2005). Some scientists, however, found that this approach may lead to incorrect conclusions, because Grime's model is concerned with the importance of competition relative to the impact of the environment, i.e. the impact of species B on A expressed as a proportion of the impact of the whole environment on A. Consequently, different indices are needed to test the theories of Grime and Tilman (Welden and Slauson 1986). Goldberg et al. (1999) conducted a meta-analysis of competition experiments and observed that competition intensity is decreasing with rising productivity. Based on these results the authors rejected both Grime's and Tilman's hypotheses. Re-analysing the data from a study by Reader et al. (1994), in which the authors also rejected Grime's theory, Brooker et al. (2005) showed that by using importance and intensity indices, both Grime's and Tilman's models could be verified with the same data set. However, there is only little evidence regarding the importance of competition along resource gradients and existing studies on single species show contradictory results. For example, Sammul et al. (2000) and Gaucherand et al. (2006) found a positive relationship for competition importance and site productivity in two grasses, while Bennett and Cahill (2012) detected a negative relationship for competition importance with site productivity and soil moisture in a grassland community. Furthermore, the use of different indices can lead to confounding effects, since not all have favourable mathematical properties like symmetry, boundedness and standardization (Díaz-Sierra et al. 2017). The lack of standardization makes comparisons among species or studies difficult. For the analysis of our data, we therefore used a new set of neighbour effect indices introduced by Díaz-Sierra et al. (2017) which combines all the above-mentioned properties. The neighbour effect importance index of these authors is the first of its kind that is standardized for plant size and thus ideally suited to separate the effects of plant interactions and other impacts on plant performance along weak environmental gradients.

Although it is unclear at which end of the productivity gradient overall competition is more intense or important, we do know under which conditions root versus shoot competition is the main mechanism determining the competitive outcome of herbaceous plants. While at lower nutrient levels root competition has greater impact on plant growth than shoot competition, both mechanisms are equally important at high nutrient levels (Kiaer et al. 2013). Recently, Foxx and Fort (2019) confirmed this pattern for different levels of water availability, with root competition being more important when water availability is poor, but more experiments are needed to clarify this topic.

Aarssen and Keogh (2002) pointed out that the majority of studies on plant competition were based on growth-related traits (e.g. plant height, biomass), while variables like

survival or fecundity are equally important to understand how plant competition works. For example, Goldberg et al. (2001) found significant negative effects on growth, although competition had no direct impact on survival in an annual community. Schiffers and Tielbörger (2006) came to similar conclusions for two other annuals. According to Aarssen and Keogh (2002) this might be due to tradeoffs in plant traits between maximizing growth and enhancing persistence by survival and reproduction. Thus, we included both growth and survival when testing the new neighbour effect indices of Díaz-Sierra et al. (2017).

To address competition intensity and competition importance along a resource gradient we identified arable plant communities as a particularly suitable study system. Plant competition has considerably changed over the past decades in arable ecosystems. Intensified fertilization and more vigorous crop varieties increasingly impair arable habitats. Thus, low competitive arable plants are suppressed both by crops and a few highly competitive weeds. This is a major reason for the severe decline of subordinate arable plant species since the 1960s (Stoate et al. 2001, Storkey et al. 2012). Conservation schemes have therefore been implemented for rare arable plants (Meyer et al. 2008). One of these species is *Arnoseris minima*, which is assumed to be a poor competitor. It is limited to unproductive sites, where competition should play no role in controlling plant communities according to Grime. However, *A. minima* has severely declined in the past decades. We therefore used this species to address the fundamental aspects of competition along productivity gradients, but also the role of above- and below-ground interactions to unravel the mechanisms leading to the decline of the species. Thus, a field experiment was conducted with different competition treatments separating above- and below-ground interactions along a productivity gradient to test the following hypotheses:

1. The *importance of competition* rises with increasing productivity, whereas the *intensity of competition* does not change for growth-related plant parameters, i.e. biomass.
2. While root competition is more significant in unproductive environments, shoot competition is more pronounced in nutrient-rich sites.
3. Severities of competition intensity and importance differ between survival and growth-related plant parameters.

Methods

Study species

Arnoseris minima (lamb's succory) is an annual plant species of the Asteraceae. In central Europe it is classified as characteristic species of the Teesdalio–Arnoseridetum plant association (Leuschner and Ellenberg 2017) which mainly occurs on sandy arable fields. *Arnoseris minima* is the only species within this genus, confined to the oceanic parts of Europe including large parts of Germany (Meusel and Jäger 1992). Here, the species has the Red List Status 2 'endangered' (Metzing et al.

2018), and it is also threatened in various other European countries (Storkey et al. 2012). Since Germany is the centre of its range and holds approximately one third of all populations, this country has a high responsibility for the conservation of the species (Ludwig et al. 2007).

Arnoseris minima mainly occurs in autumn-sown cereals on sandy soils with low concentrations of nutrients and low alkalinity. According to Schneider et al. (1994) and Kästner et al. (2001), it germinates in autumn and spring. The species is a rosette plant and reaches maximum heights of 10–25 cm. Vegetative growth of the rosettes is observed in April, followed by shoot development in mid-May and flowering from June on. The tap root system usually reaches depths of 10–35 cm up to 50 cm (Kästner et al. 2001), while Kudoke (cited in Schneider et al. 1994) reported depths of only 8 cm.

Study sites

To test the basic theory of competitive interactions using the study species *A. minima*, we performed an experiment on 18 arable fields in the natural subunit Franconian Basin between Bamberg and Roth in N-Bavaria (Supporting information), from early April till early July 2019. Altitude of the sites was 288–412 m, with higher ones in the south, and lower ones in the north. Mean annual temperatures ranged between 9.0 and 9.6°C and mean annual rainfall was 655–757 mm (1988–2018; Supporting information). During the study period in 2019 temperatures deviated from these long-term values as follows (average over all sites): April +1.3, May −2.7 and June +3.6°C, while precipitation showed the opposite pattern being lower in April (−16 mm) and June (−33 mm), and higher in May (+15 mm).

The Franconian Basin is part of the natural unit 'Keuper-Lias-Land', where Keuper sandstone supports acidic and coarse grained cambisols (Schilling and Hammerl 2002). Soil samples from the study sites had sand proportions of 67–87% and pH values ranging between 3.6 and 6.1 (Supporting information). The main criterion for choosing the sampling sites was sufficient abundance of the study species, so that the experiment would not threaten the populations. On seven arable fields, *A. minima* was reintroduced in 2017 or 2018, while the other fields still had natural populations. Furthermore, the sites also differed management. Eight sites were cultivated with autumn-sown cereals, mainly rye, while seven were fallows with last soil cultivation in autumn 2018, called 'young fallows' in the following. The remaining three sites had been fallow for more than one year ('old fallows').

Experimental setup

To separate the effects of root and shoot competition the 'target technique' was used (McPhee and Aarssen 2001), where target plants of the study species are separated from the surrounding vegetation by the following treatments:

1. … growing without roots and shoots of neighbours (*no competition*, NC)
2. … interacting with roots, but not with shoots of neighbours (*root competition*, RC)
3. … interacting with shoots, but not with roots of neighbours (*shoot competition*, SC)
4. … interacting with roots and shoots of neighbours (*full competition*, FC)
5. … equipped with a weed fleece to suppress competitors (*reduced competition*, RedC)

In all treatments except for the full competition treatment neighbouring plants in a radius of approximately 15 cm were cut and a 12.5 × 12.5 cm weed fleece was placed around the target plant to prevent other plants from germination. To exclude root competition, partitions consisting of plastic tubes (diameter 16 cm, depth 18 cm) were established in the soil around the target plants. Above-ground partitions made of inverted wire mesh funnels (diameter 16 cm at the ground, and 50 cm at the top, height 50 cm) were installed to exclude shoot competition; to exclude above- and below-ground competition both methods were combined (Fig. 1). The effect of the weed fleece was investigated in the fifth treatment. We investigated three plants of *A. minima* per treatment and field, at sites with very small populations plant numbers were reduced (Supporting information).

To ensure comparability within the sites, plants with initial rosette diameters around 2 cm were selected and treatments were randomly assigned to the plants. At each site three replicates of the five treatments were established within plots of 5 × 5 m. The plots were at least 5 m apart along the field edge. The experiment was set up at the beginning of April 2019 (sites 1–15: 02–05.04.2019, sites 16–19: 10–11.04.2019) and plant performance measurements were conducted monthly (early May: 06–09.05.2019; early June: 03–06.06.2019). Plant height, rosette diameter, number of primary shoots, number of flowers, number of seed pods and above-ground biomass were measured as proxies of fitness. The results shown in the study, however, focus on above-ground biomass, since all other measured plant traits followed similar patterns as biomass in the competition treatments. The biomass was harvested in early July 2019, shortly before the end of the experiment and the harvest of crops; it was dried at 65°C for 48 h before weighing.

Calculation of competition intensity and importance

The competitive response was calculated using a *neighbour effect intensity index* with additive symmetry ($NInt_A$), and a *neighbour effect importance index* with additive symmetry ($NImp_A$; Díaz-Sierra et al. 2017). These indices show suitable mathematical properties, mainly standardization and symmetry with $NImp_A$, being the first index with a standardization for size. This allows an unbiased comparison between competition intensity and importance. The indices range from −1 to +2, with negative values indicating competition and positive values facilitation. The indices therefore might appear asymmetric, however this is not the case. As long as the effect of facilitation on target plant performance is smaller or equal than the effect of competition, the indices render the same absolute values (from −1 to +1). That is, the absolute limit of competition is when exclusive competition occurs and the plant dies due to the competitive effects of neighbours. From an additive perspective, the same intensity of facilitation would cause the plant with neighbours to double its biomass compared to the plant without neighbours. Above
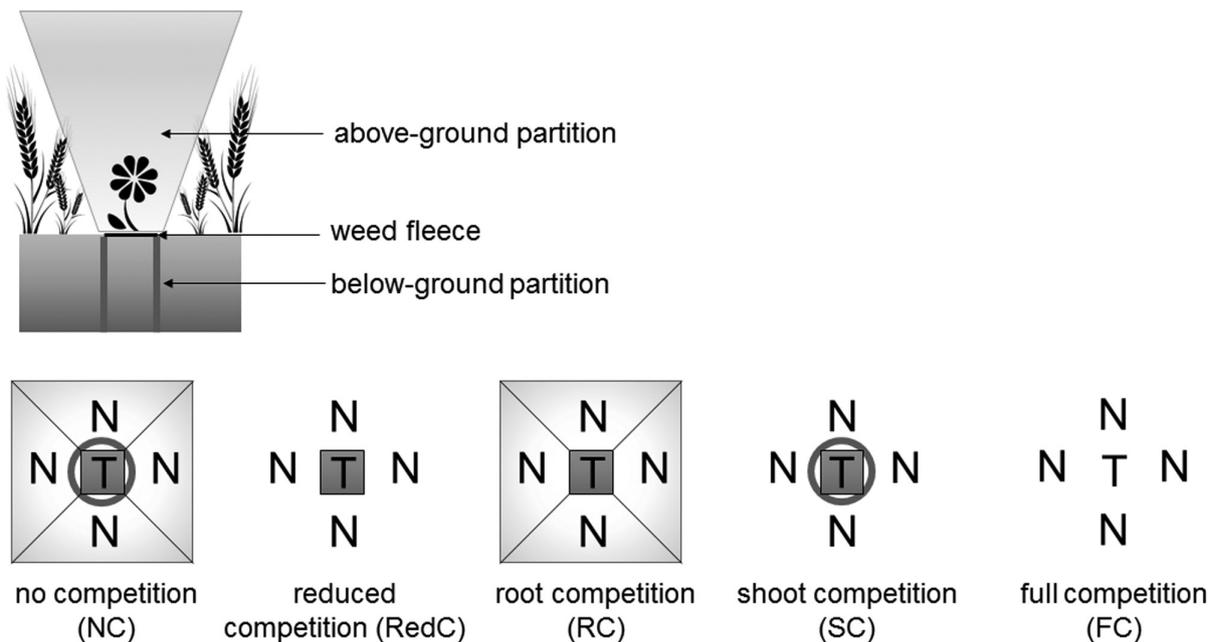

Figure 1. Design of the five competition treatments; T = target plant, N = neighbouring plants, with circles indicating below-ground partitions, light grey squares representing above-ground partitions and dark grey squares describing weed fleece.

this threshold, there is no possible comparison between the intensity of facilitation and competition from an additive perspective of plant–plant interactions effects on biomass. Facilitation, however, can (otherwise than competition) theoretically increase target plant performance indefinitely, therefore the boundary for facilitation is set to +2 to account for such a scenario. So even though the boundaries of the indices are uneven they are still symmetric, since the underlying assumption is that facilitation and competition are processes that are intrinsically not symmetric from an 'additive' perspective. However, if these extreme facilitative effects occur in an experimental treatment where both facilitative and competitive effects occur, caution should be guaranteed, as mean treatment values will be biased towards less competition or more facilitation than it really was the case.

Competition intensity is the competitive effect neighbours have on the target plant, and it is calculated with the following formula:

$$\text{NInt}_A = 2 \times \Delta P / (P_{-N} + |\Delta P|)$$

where ΔP is the total impact of neighbours on the performance P of a target plant ($\Delta P = P_{+N} - P_{-N}$; P_{+N} = performance with neighbours; P_{-N} = performance without neighbours, in our case the no competition (NC) treatment), and $|\Delta P|$ is its absolute value.

Competition importance is the reduction of plant performance due to competition relative to the environmental constraints and is calculated as follows:

$$\text{NImp}_A = 2 \times \Delta P / (2MP_{-N} - P_{-N} + |\Delta P|)$$

where MP_{-N} is the maximum performance of a plant without neighbours. This maximum performance corresponds to the environmental optimum where the growing conditions for the species are ideal. To calculate NImp_A for the biomass, this value was set to 6 g, i.e. the maximum biomass found for individual plants of *A. minima* in a pot experiment conducted by Kulp (1991); furthermore, own pot experiments with seeds from the study populations showed similar maximum biomass (M. Lang, unpubl. results). Both indices have been calculated per plot and for all competition treatments for single plant pairs. To facilitate understanding, NInt_A and NImp_A are called *competition intensity* and *competition importance* throughout the study.

Statistical analyses

Statistical analyses were conducted using R (<www.r-project.org>). We mainly calculated linear mixed effects models (LME) for the analyses. Since we used data from the plot level 'site' was included as random effect to account for the fact that the three replications at each site (i.e. plots) in fact were pseudoreplications (Pinheiro and Bates 2004). Models were implemented in R using the function *lmer* of the package *lme4* (Bates et al. 2015). To check for significance of variables and factorial analyses, the function *Anova* from the package *car* was used, which actually calculates a Wald chi square test. For the regressions with $\text{NInt}_A/\text{NImp}_A$ as a response variable, the productivity was set as explanatory variable and site included as random effect. As interactions between the environmental variables made it difficult to consider only one of them to be representative of the productivity, target plant biomass without competition (NC) was used as a proxy, as done by Brooker et al. (2005). Furthermore, since standing biomass of arable fields is strongly influenced by agricultural management, using this proxy seems to be reasonable.

In the factorial analysis, the treatments were used as predictor and site included as random effect. Post hoc tests for factorial analysis were performed using the function *glht* of the package *multcomp* (Hothorn et al. 2008), which does multiple comparisons.

To validate model assumption Q–Q plots were applied as well as plots of fitted values versus residuals using base R and the package *DHARMa* (Hartig 2019). R^2 values were calculated with the function *r.squaredGLMM*, implemented in the package *MuMIn* (Barton 2019). This function calculates two R^2 values, one is called R^2 marginal (R^2_m) which represents the variance explained by the fixed effects and R^2 conditional (R^2_c) which explains the variance of the full model, including fixed and random effects.

The analyses showed that survival of target plants was independent of the competition treatments (except for reduced competition). Therefore, we had to exclude target plants which senesced during the course of the study from the analyses.

Results

Effect of competition treatments

The five competition treatments had marked effects on the performance of *A. minima* (Table 1). When grown without competition, target plants produced an average biomass of 2.03 ± 0.16 g (mean $\pm$ SE). While shoot competition (SC) only slightly reduced the average biomass (1.44 ± 0.13 g), root competition (RC) caused a substantial decline of this feature (0.71 ± 0.11 g). Full competition (FC) led to the lowest biomass of target plants with an average of 0.34 ± 0.07 g. No significant difference was observed between full and reduced competition (0.54 ± 0.09 g). Competition intensity (NInt_A) calculated with biomass showed the same pattern regarding the difference between competition treatments (Table 1). Competition importance (NImp_A), however, only differed between treatments with and without root competition, being significantly lower in absolute values for the shoot competition treatment compared to full, root and reduced competition (Table 1); for mean values per site see Supporting information.

Survival of target plants with reduced competition (RedC) differed significantly from target plants without

Table 1. Effect of competition treatments on different fitness parameters of Arnoseris minima; $NInt_A$ and NImpA were calculated with biomass data; mean ± SE; FC, full competition; RedC, reduced competition; RC, only root competition; SC, only shoot competition; NC, no competition. Linear mixed effects model (LME) with site as random factor; biomass data were square root transformed prior to analysis to meet model assumptions; model structure for survival: generalized linear mixed effect model (GLME) with site as random factor; Wald X^2 test followed by post hoc Tukey test were performed, for statistics on Wald X^2 test see Supporting information different letters show significant differences between competition treatments at $p < 0.05$.

Response	Treatment				
	FC	RedC	RC	SC	NC
Survival (%)	88 ± 5[ab]	74 ± 6[a]	90 ± 4[ab]	84 ± 5[ab]	96 ± 3[b]
Biomass (g)	0.34 ± 0.07[a]	0.54 ± 0.11[ab]	0.71 ± 0.11[b]	1.44 ± 0.13[c]	2.03 ± 0.16[d]
$NInt_A$	−0.87 ± 0.03[a]	−0.81 ± 0.04[ab]	−0.68 ± 0.07[b]	−0.29 ± 0.08[c]	−
$NImp_A$	−0.30 ± 0.03[a]	−0.27 ± 0.03[a]	−0.25 ± 0.03[a]	−0.12 ± 0.03[b]	−

competition (NC), but there were no significant differences between all other treatments (Table 1). The intensity of competition ($NInt_A$) as well as the importance of competition ($NImp_A$) were significantly lower for survival (absolute values) than for biomass (Fig. 2). Mean competition importance for the full competition treatment was −0.30 ± 0.03 when calculated for biomass and −0.09 ± 0.05 when calculated for survival. Average competition intensity was −0.77 ± 0.03 for biomass and −0.04 ± 0.08 for survival. Both indices show that competition essentially impacted plant growth, while the effect on survival was almost negligible.

Competition along the productivity gradient

Competition intensity ($NInt_A$) calculated with biomass was constant along the productivity gradient for full competition and root competition (Fig. 3a). However, for shoot competition we found a negative relationship with productivity (Fig. 3a). Therefore, shoot competition was more intense when productivity was higher.

Competition importance ($NImp_A$) showed a negative relationship with site productivity independently of the competition treatments (Fig. 3b). Slopes of the regression were equally steep for root and full competition but gentler for shoot competition (Table 2). The intercept did not differ between treatments and was not different from zero (Table 2).

Discussion

Competition along the productivity gradient

The results of our study indicate that competition intensity did not change across different levels of productivity when plants experienced full competition. On the other hand competition importance, reflecting the impact of neighbours on the performance of *A. minima* relative to environmental stress, significantly increased with site productivity (absolute values). At the unproductive end of the gradient competition importance was close to zero. Although competition intensity was strong at the unproductive sites, the reduction in plant biomass induced by competition was negligible compared to the reduction due to other factors such as environmental stress. This verifies the expectation that competition importance and intensity must not necessarily be correlated (Welden and Slauson 1986), as shown by Brooker and Kikvidze (2008). Thus, our results confirm our first hypothesis, and they are also consistent with both the *life history trade off theory* of Grime (1979) and the *resource ratio theory* of Tilman (1982).

Rees (2013) argued that the theoretic frameworks of Grime and Tilman are generally inappropriate to explain the results of experiments along productivity gradients, since they are primarily concerned with large-scale, between-habitat patterns of community structures. Most relevant experiments, however, took only short time periods and examined the performance of single plants. Rees (2013), therefore, developed
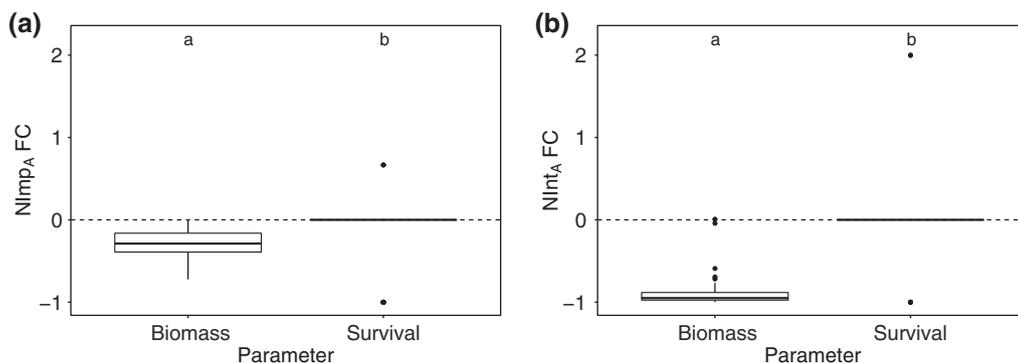

Figure 2. The effect of biomass and survival on competition importance (a) and competition intensity (b) of target plants with full competition (FC) – negative values show competition, positive ones facilitation. Linear mixed effects model (LME) with site as random factor; different letters above boxplots show significant differences ($p < 0.05$).
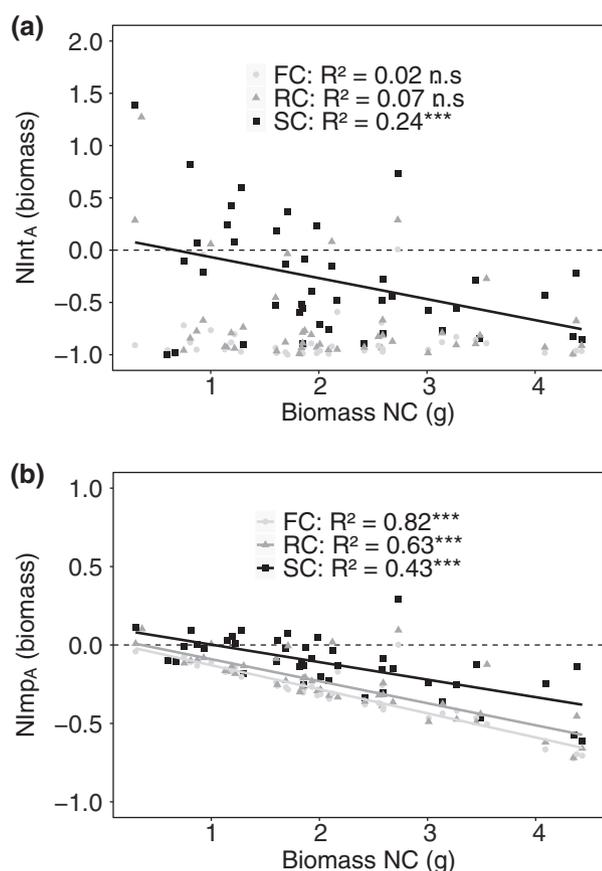
Figure 3. Relationship of biomass of *Arnoseris minima* without competition (NC) as a proxy for site productivity with (a) competition importance (NImp$_A$), and (b) competition intensity (NInt$_A$). Negative values show competition, positive values show facilitation; ***=p < 0.001; model structure: linear mixed effects model (LME) with site as random factor; to meet model assumptions, data for NInt$_A$ were log(x+1)-transformed for NC and RC but not for SC prior to analysis; shown are untransformed data; For statistics on regression models see Supporting information.

a model for resource competition, suitable for the interpretation of such experiments. According to this model, competition intensity should increase with productivity, when also the density of competitors increases with productivity. In our study, competition intensity remained unchanged along the productivity gradient, while plant coverage around the target plants showed no correlation with site productivity. Thus, our results also agree with the model of Rees (2013).

Root versus shoot competition

Averaged across all sites, root competition was the dominant form of competition determining plant performance. This was true for competition intensity as well as for competition importance. When plants where competing for soil resources the direct impact of neighbours on targets (i.e. competition intensity) did not change along the productivity gradient. Competition intensity of the shoot competition treatment, however, increased with rising productivity, so that it was as strong as root competition intensity at the most productive sites. At the most unproductive sites, shoot competition intensity was close to zero or had even a facilitative effect on target plant growth. This would be in line with the stress-gradient hypothesis (Callaway 1995; Callaway and Walker 1997). However, since standing biomass at the low productive sites was quite low, facilitative effects due to changes in microclimate were unlikely. The apparent facilitative interactions where probably caused by differences in the soil conditions at the plot level leading to random differences in biomass of shoot competition and no competition treatments. At the more productive sites, however, competition for light was strong.

Although shoot competition intensity increased with rising productivity, there was no shift from root competition being more important at low productivity to shoot competition more important at high productivity, as assumed in our second hypothesis. Probably, the productivity gradient in our study was not long enough to cover these extremes. Even at the most productive sites plant growth was too low to produce a standing biomass able to reduce light to a level below the growth limitation induced by soil resources (Kiaer et al. 2013).

In our study, the strong effect of root competition on plant performance was most likely increased by the low precipitation in the study period in summer 2019 (i.e. 35 mm below the average 1988–2018), and the uneven distribution of rainfall (i.e. no rain at the beginning and towards the end of the study period). In years with higher amounts and a more even distribution of precipitation, root competition might have been weaker leading to an additive interaction of shoot and root competition, especially towards the productive end of the gradient. A shift to a positive interaction on even more productive sites than the ones studied is unlikely. Cahill (2002) stated that positive interactions would be found in species which have the potential to reach the plant canopy. Due to the rosette growth form of *A. minima*, this condition is

Table 2. Regression of NImp$_A$ with biomass without competition (biomass NC), shoot and root competition treatments (dummy variables) and their interaction with biomass NC; model structure: linear mixed effects model (LME) with site as random factor; significant values in bold.

Response	Coefficient	Estimate ± SE	df	t value	p value
NImp$_A$	Intercept	0.054 ± 0.040	95.8	1.355	0.179
	SC treatment	0.088 ± 0.050	105.2	1.754	0.082
	RC treatment	0.018 ± 0.051	109.3	0.351	0.726
	biomass NC	−0.169 ± 0.017	110.8	−10.037	**< 0.001**
	SC × biomass NC	0.044 ± 0.021	105.2	2.041	**0.044**
	RC × biomass NC	0.016 ± 0.021	110.8	0.774	0.441

impossible to fulfil. So even though shoot competition intensity increased with productivity, its impact remained small due to the negative interaction of shoot and root competition. Therefore, our second hypothesis must be rejected.

Different reaction of growth and survival

The third hypothesis was supported by the results, since survival was affected only very slightly by competition, with competition intensity close to zero independently of its type. Growth, however, was strongly impacted by competition. Goldberg et al. (2001) argued that distinguishing resource retention and acquisition could provide an explanation for the differences in the responses of survival and growth related traits to competition. When plants experience nutrient stress, they reallocate nutrients and, therefore, the uptake of further nutrients to secure survival might be of minor importance (Chapin 1980). For growth, however, resource uptake must exceed the level necessary for survival. Under conditions where resources are limiting the resource uptake by neighbouring plants will therefore impact the growth of a target plant stronger than survival.

Additionally, it is well-known that emergence and recruitment are critical stages in plant life history (Goldberg et al. 2001, Aarssen and Keogh 2002). Since we used already established seedlings, we cannot account for processes which took place before the study started, although early competition is decisive for establishment of *A. minima*. Evidence towards this direction was found by L. Bäumler (unpubl. results), where numbers of fertile individuals of *A. minima* per plot were higher when the standing biomass was low (estimated by plant coverage multiplied by average height). Four of the six sites used in this experiment were also included in our study, so the results are comparable. For population development survival of seedlings seems therefore to be more important than survival of established plants.

At very unproductive sites competition is unimportant for the decline of *A. minima*. In the range of the study sites even at the more productive sites the importance of competition stayed intermediate. The extensive use of herbicides as well as the abandonment of marginal lands must be more important for reducing *A. minima*. At the most unproductive study sites root competition was the major factor determining plant performance. There, the populations of *A. minima* will probably persist, because there is little evidence that root competition leads to shifts in community composition (Lamb et al. 2009). However, we conclude that there was most likely a shift from symmetric to asymmetric competition along the production gradient because shoot competition was increasing with productivity. This could eventually lead to competitive exclusion of *A. minima* at the more productive sites (DeMalach et al. 2016).

Conclusion

Using the rare arable plant species *Arnoseris minima*, we addressed fundamental principles of competition along a productivity gradient. Both the *life history trade off theory* of Grime and the *resource ratio theory* of Tilman were verified in a large-scale field study when using the appropriate competition index. Thus, the relationship of competition importance with productivity confirmed Grime's theory, whereas the lack of a relationship of competition intensity with the productivity gradient agrees with Tilman. Root competition was the main mechanism determining target plant performance. Shoot competition intensity increased with rising productivity, while it remained of minor importance compared to root competition intensity. This could be due to the generally low water- and nutrient-availability at our study sites. While plant growth was strongly impacted by competition this was not the case for survival. Thus, our study improves the understanding of intensity and importance of competition for plant species under varying environmental conditions.

Author contributions

Fabian Sauter: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Harald Albrecht**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Johannes Kollmann**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Marion Lang**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.rn8pk0p8z> (Sauter et al. 2021).

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