Effects of root competition and soils on seedling establishment at the ecotone between an arid grassland and succulent shrubland in South Africa

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Abstract

Questions: What are the effects of root competition from mature plants and soil type on the survival and growth of dominant grass and succulent shrub seedlings at an ecotonal site between arid grassland and succulent shrubland? Do these factors explain the occurrence of separate grass-dominated and shrub-dominated communities along the ecotone?

Location: Ecotone between Bushmanland arid grassland and Namaqualand succulent shrublands in the Karoo, South Africa.

Methods: Seedlings of *Stipagrostis brevifolia,* a perennial C_4 grass, and *Ruschia robusta*, a leaf-succulent shrub were transplanted into naturally occurring openings within separate *Stipagrostis brevifolia* and *Ruschia robusta* communities. The effects of root competition were tested by exposing seedlings to roots of neighbouring adult plants or by excluding the influence of neighbouring roots using metal partitions. The influence of soil on the survival and growth response of seedlings was tested by comparing the response of each species grown in soil of their own community with their response when grown in soil of the other community.

Results: All *S. brevifolia* seedlings died within the first 3 mo of the experiment, irrespective of competition exclusion or whether they were grown in grassland or shrubland soils. Root competition from mature plants reduced the survival of *R. robusta* seedlings in the grass community, but not in the shrub community. When seedlings of *R. robusta* were not exposed to root competition, their survival and biomass in the grass community soil type did not differ from that in the shrub community soil type.

Conclusions: Excluding root competition in the grass community provided favourable conditions for *R. robusta* seedlings to establish, suggesting that root competition from the grass is more important in maintaining separate grass communities, and that any differences in soil properties are less important in influencing such processes. Our study presents an example where a species' fundamental niche may be differerent from its realized niche, as a result of competitive interactions.

Introduction

The concepts of fundamental and realized niche reflect the phenomenon that the limits of a plant's distribution are not simply set by environmental limitations, but direct interference between neighbouring plants may impose patterns on the vegetation (Yeaton & Cody 1976; Grime 1977; Grace & Tilman 1990; Damgaard 1998; Dunnett & Grime 1999). Although the relative importance of biotic and abiotic factors varies at different scales, soil properties, microclimate and competition have all been reported as being important in structuring plant communities at local scales in many ecosystems (El-Ghani 2000; Buxbaum & Vanderbilt 2007; Bisigato et al. 2009). Distinct zonation of species is often thought to follow environmental gradients, but it is now widely accepted that measurements of

edaphic and climatic tolerances of species are imperfect predictors of their distributions (Grime 1977; Grace & Tilman 1990; Dunnett & Grime 1999; Silvertown et al. 1999). Whether species would co-exist or segregate into different communities thus depends on competitive interactions, which largely govern inter-specific dynamics (Hardin 1960; Brown 1971; Rosenzweig 1981; Gordon 2000; Silvertown 2004). Competitive interactions between plants have received much attention in community ecology, and several competition and co-existence models have been postulated and supported, e.g the classical niche partitioning along various environmental niche axes to facilitate co-existence of species (Cody 1986; Sala et al. 1989; Gordon 2000; Silvertown 2004), and the competitive exclusion principle (Hardin 1960; Brown 1971; Armstrong & McGehee 1980; Gurevitch 1986).

In arid and semi-arid environments, competition for soil resouces is argued as the most pervasive factor structuring plant communities (Yeaton & Cody 1976; Fonteyn & Mahall 1981; Yeaton & Esler 1990; Damgaard 1998). There is enough evidence in the arid and semi-arid environments of the Karoo to support the hypothesis that competition occurs, among perennial shrubs (Yeaton & Esler 1990; Esler & Cowling 1993; Carrick 2003), between perennial shrubs and annuals (Cunliffe et al. 1990) and between succulent shrubs and perennial grasses (Shiponeni et al. 2011), but abrupt boundaries between plant communities along edaphic discontinuities have also been demonstrated (e.g Lloyd 1989; Milton et al. 1997). The vegetation along the ecotone between Bushmanland arid grassland and the succulent shrublands of Namaqualand, in the Karoo region of South Africa, is characterized by segregated grassland and leaf-succulent shrubland communities, but also communities in which grasses and succulent shrubs co-occur (Shiponeni et al. 2011). Understanding the non-random distribution patterns in vegetation is one of the key objectives in ecology. This is particularly important within ecotonal regions where the sensitivity of vegetation to environmental change is expected to be highest (Lechmere-Oertel & Cowling 2001). The distribution of perennial C_4 grasses in the Karoo (e.g Stipagrostis spp.) is generally associated with deeper, sandy soils, in relation to the succulent shrubs on shallower, more loamy soils (Lloyd 1989; Carrick 2001; Mucina 2006). At the ecotone, however, underlying physical and chemical soil properties across community gradients of grasslands and succulent shrublands explained $\leq 15\%$ of the variation in the vegetation (Shiponeni 2007), indicating that such soil preferences contribute little to the observed vegetation patterns. We hypothesized that inter-specific competitive interactions between ecotonal species largely explain the patterns evident in these vegetation communities.

Competition, however, needs to be confirmed through experiments, in order to distinguish between the effect of habitat preference and competitive exclusion (Gurevitch 1986). Such experiments usually focus on seedling establishment since this is a critical life-history stage for persistence (Snaydon & Howe 1986; Aguilera & Lauenroth 1993; Davis et al. 1998; Sanchez & Peco 2004). In this study, we combine reciprocal transplanting of seedlings (e.g Esler & Cowling 1993; Crain et al. 2004) with a root exclusion treatment (e.g. Snaydon & Howe 1986; Aguilera & Lauenroth 1993; Sanchez & Peco 2004) in a field experiment within communities of grass and succulent shrubs. This was done in order to investigate the influence of soil type as well as root competition from mature plants on the establishment of seedlings of the dominant grass and succulent shrub species. In this way, two hypotheses were tested simultaneously by transplanting seedlings, with and without the exclusion of root competition from the established adult plants in the two communities. First, we tested whether seedlings of the C_4 grass Stipagrostis brevifolia or of the succulent, facultative CAM shrub Ruschia robusta would establish better when grown in soils of their own community than when grown in soils where the other species is dominant. Second, we tested whether root competition from established adult plants inhibited the establishment of seedlings.

Methods

Study area

The study was carried out on the farm Kougoedvlakte (18°26′ E, −30°20′ S), along an ecotonal border between Bushmanland arid grassland and Namaqualand succulent shrubland, in the Northern Cape Province of South Africa. Climatically, this area lies in a zone between the predominantly winter rainfall Succulent Karoo biome in the west and the predominantly summer rainfall Nama Karoo biome in the east. Rainfall patterns at the ecotone show no marked seasonality and the ecotonal region receives both winter and summer rainfall (Fig. 1). Annual average rainfall is 116 mm (1984–2006), and rainfall between years is extremely variable, with a coefficient of variation (CV) of 41%. Namaqualand is dominated by granitic gneisses which decay to form rich soils, whereas the quaternary sands and Karoo Sequence shales of Bushmanland give rise to weak and structureless clay and sandy soils (Ellis & Lambrechts 1986). Lloyd (1989), working in the Vaalputs area which also forms part of the ecotone, described broad underlying soil factors. She identified light brown soil, characterizing shrub communities close to areas of rocky outcrops, red-brown aeolian sand associated with grass communities, and intermediate sands in the transition zone between light-brown and red-brown sands. Soils in
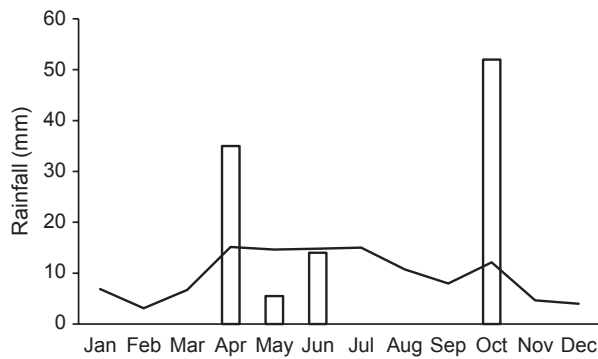
Fig. 1. Mean monthly rainfall (solid line) for the period 1984–2006 and the monthly rainfall (bars) during 2005 at De Riet, a farm adjacent to the study site. Mean annual rainfall = 116 mm; CV = 41%.

ecotonal communities are generally low in nutrients, and contain $\leq$ 1% nitrogen (February et al. 2011).

The vegetation along the ecotone is transitional between arid Bushmanland grassland and Namaqualand succulent shrubland, and is composed of grass communities, succulent shrub communities and occasionally of mixed grass/shrub communities. The grass component is represented primarily by one of the dominant Bushmanland perennial C_4 grass species, *S. brevifolia*. The dominant shrub species, *R. robusta*, belongs to a group of leaf-succulent plants in the family Aizoaceae. Structurally, these communities are described as low vegetation ($\leq$ 1 m in height), and sparsely vegetated (Mucina 2006). Two representative communities, dominated by *S. brevifolia* and *R. robusta*, respectively, about 1 km apart, were selected for the present study. Vegetation cover and composition in these two communities (Fig. 2) is similar to that observed along the ecotone. The rangeland at the study site, and along the
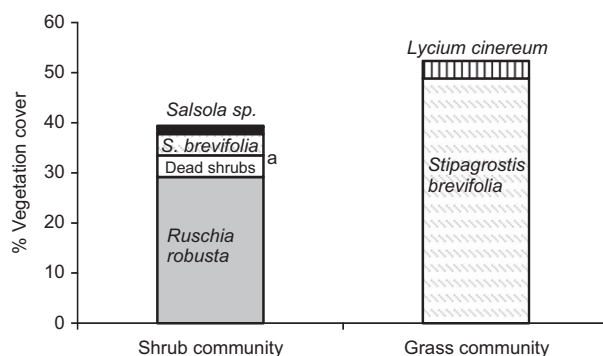

Fig. 2. Vegetation canopy cover (%) and composition in the two communities used for the seedling transplant experiment on Kougoedvlakte farm (extracted from Shiponeni et al. 2011). [a] Skeletons of dead *Ruschia robusta* shrubs made up the second most dominant cover in the shrub community and this value was thus included.

ecotone, is privately owned and mainly grazed by domestic livestock (primarily sheep) following commercial management practices and moderate stocking rates (Hoffman & Ashwell 2001).

The seedling transplant experiment

Seeds of *S. brevifolia* and *R. robusta* were collected from the field and sown on the 16 February 2005 in seedling trays comprised of compartments 3 × 3-cm wide and 6-cm deep, using soil collected in a riverbed near the study area. In each seedling tray, three seeds of one species were sown in each compartment, and the trays were kept in a glasshouse at the University of Cape Town. The seedling trays were well watered to encourage germination. Germination commenced 2 d after sowing for *R. robusta*, and 4 d after sowing in the case of *S. brevifolia*. Where more than one seedling emerged, the first seedling was maintained and the rest were removed from the compartment. The seedlings were watered daily for 2 wk, after which watering was reduced to once every second day. After 4 wk, watering was reduced to every third day until the seedlings were transplanted into the field on 28 April 2005.

In the field, ten naturally occurring gaps between established plants, of at least 50 × 40 cm in size, were identified in both *S. brevifolia* and *R. robusta* communities (referred to as grass and shrub communities, respectively). In each community, five of these gaps were randomly allocated to 'neighbour root exclusion plots' and five to 'neighbour root competition plots'. Thus, the transplanted seedlings of each species were either exposed to or excluded from the roots of adult plants in a *S. brevifolia* community or a *R. robusta* community. For the 'neighbour root exclusion plots', steel boxes 50 × 40-cm wide and 30-cm deep, open at the top and bottom, were carefully sunk into the ground with as little soil disturbance as possible. These structures excluded roots of the surrounding vegetation in the surface 27 cm of soil from competing for soil resources with the transplanted seedlings in these plots (Snaydon & Howe 1986). Similar boxes were used in control plots ('neighbour root competition'), where seedlings were allowed to grow in the presence of roots of established vegetation. These boxes, however, were only 3-cm deep (50 × 40 × 3 cm) and were not sunk into the ground, but placed on the soil and thus protruded above the ground to a similar height as the 'root exclusion' boxes. This experimental design allows the effects of root competition to be distinguished from those arising as a result of differences in soil properties between the two communities. The proximity of the two experimental communities, the comparable vegetation structure and cover, as well as the naturally occurring spaces of about equal size, meant that other environmental factors such as light and wind

conditions were unlikely to vary significantly between sites. Thus, any variation in seedling growth under 'neighbour root exclusion plots' were assumed to be due to differences in soil conditions.

Seedlings of both species were transplanted into each plot, in regular patterns 10-cm apart, and a minimum of 5 cm from the edge of the box. Surviving seedlings from the glasshouse allowed for a maximum of eight seedlings of *S. brevifolia* to be transplanted in each box, whereas sufficient seedlings of *R. robusta* were available to allow ten seedlings per box. The position of each individual within the boxes was predetermined randomly. The seedlings were watered immediately after transplanting, but the soil was also still moist from heavy showers received 2 wk prior to transplanting. The amount of water provided approximated an average rainfall 'event' commonly experienced in the region. This amounted to 2.5 L water per box, which is equivalent to a rainfall event of 10 mm. A chicken wire fence (with a mesh size of 1.5×2.0 cm) was erected around each box to prevent damage to seedlings by domestic livestock and other animals. Seedlings were watered on the following 2 d, and then at 2-day intervals until day 11 after transplanting, when the seedlings were counted and measured for the first time. The transplants were watered (2.5 L per box) for the last time 2 wk later, when they were also counted and measured for the second time. The monthly rainfall that occurred during 2005 is shown in Fig. 1.

Seedlings were monitored for survival and growth on the following dates: 09 May 2005, 23 May 2005, 11 June 2005, 27 July 2005, 07 September 2005 and 21 January 2006. Growth was monitored in terms of height of the seedlings for both species and number of leaf pairs for *R. robusta*. At the end of the experiment (21 January 2006), above-ground and below-ground biomass of surviving seedlings was harvested, washed free of sand and dried for 48 h at 70 °C for dry biomass determination.

Data analysis

Stipagrostis brevifolia seedlings experienced very high mortality early in the experiment, regardless of competition or community type in which they were grown. Because of this, there were insufficient seedlings surviving beyond the first 44 d of the experiment for meaningful statistical analyses. For competition in particular, this time period may be too short to have a measurable effect.

Binomial logistic regression analyses were applied to shrub seedling survival data at the end of the experiment using the binary logistic function in IBM SPSS Statistics v. 19 (SPSS, Chicago, IL, US), to test for effects of root competition and the effects of soils in which the seedlings were grown. ANOVAs on growth and biomass data, as described

below, were conducted using Statistica v. 7, (StatSoft Inc., Tulsa, OK, US). Normality was tested using the Kolmogorov–Smirnov and Lilliefors tests and homogeneity of variance was tested with Levene tests. The number of leaf pairs and the biomass data were square-root-transformed, while height data were log-transformed to meet normality and homogeneity of variance assumptions. *Ruschia robusta* seedlings exposed to root competition in the grass community experienced very high mortality (only four seedlings survived). This treatment therefore provided insufficient replication for height, growth and biomass data and was excluded from further analyses. One-way ANOVAs were conducted on height, growth and biomass data to test for (1) mean differences between seedlings grown under competition exclusion in the grass community and competition exclusion in the shrub community (effects of underlying soils on *R. robusta* seedlings), and (2) mean differences between seedlings grown under competition exclusion in the shrub community and competition plots in the shrub community (conspecific competition in shrub community).

Results

Almost all *S. brevifolia* seedlings died in the first 3 mo of the experiment, with only one seedling surviving to the end of the experiment (Fig. 3). The seedlings that survived the longest were in the competition exclusion plots (Fig. 3).

Competition from established grass vegetation significantly affected the survival of *R. robusta* seedlings (binary logistic model, $\chi^2 = 36.50$, $df = 1$, $P < 0.0005$). The negative B value (-3.201) and the odds ratio indicate that *R. robusta* seedlings exposed to root competition from established grass are less likely to be alive by a factor of 0.041 (95% CI 0.012–0.141) than in the absence of competition from neighbouring roots. Only 8% (four seedlings) of *R. robusta* seedlings exposed to competition in the grass community survived to the end of the experiment, compared to 77% seedling survival in the 'competition exclusion plots' in the same community (Fig. 3).

In the shrub community, root competition had no effect on the survival of *R. robusta* seedlings (binary logistic model, $\chi^2 = 0.281$, $df = 1$, $p = 0.6$), but the seedlings exposed to root competition from conspecific adult shrubs had significantly reduced height (one-way ANOVA, $F_{(1,8)} = 19.57$, $P = 0.002$), fewer leaves ($F_{(1,8)} = 15.49$, $P = 0.004$) and lower biomass ($F_{(1,8)} = 22.42$, $P = 0.001$; Figs 4 and 5).

Soil type did not reliably predict *R. robusta* seedling survival (binary logistic model, $\chi^2 = 0.173$, $df = 1$, $P = 0.68$) seedling survival of 81% in own community vs. 77% in grass community (Fig. 3), nor was there a difference in leaf
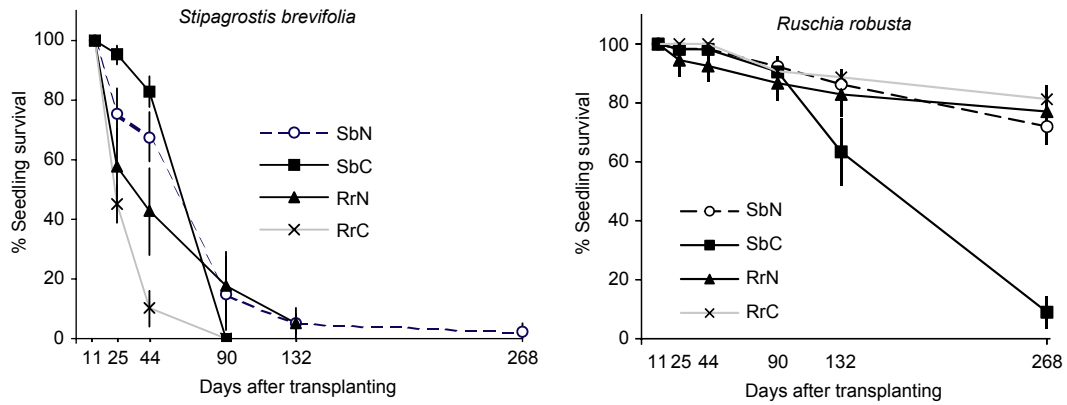
Fig. 3. Survival of seedlings of the grass *Stipagrostis brevifolia* and the succulent shrub *R. robusta* in grass and shrub communities in competition exclusion plots and competition plots in both communities. Data are means (±1 SE). SbN = no competition in the grass community, SbC = Competition in the grass community, RrN = no competition in the shrub community, RrC = Competition in the shrub community.
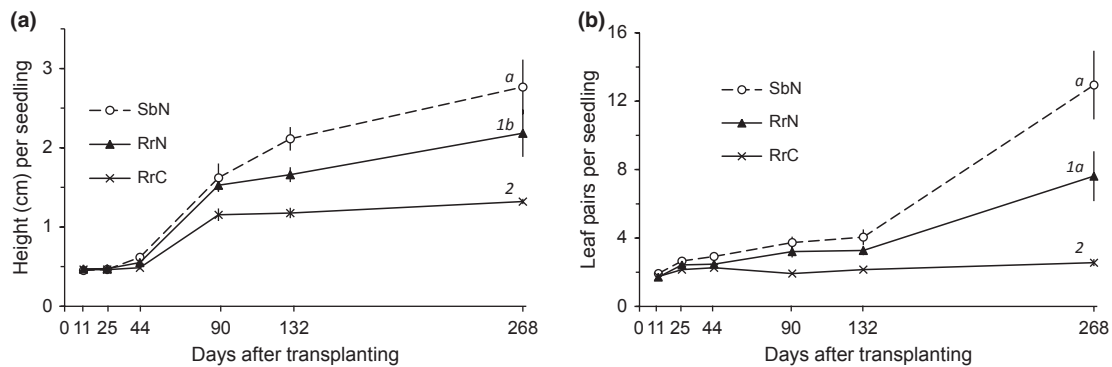

Fig. 4. Height of surviving seedlings **(a)** and number of leaf pairs **(b)** for *R. robusta* seedlings grown in competition exclusion plots in the grass community (SbN), competition exclusion plots in the shrub community (RrN), and in competition plots in the shrub community (RrC). Data are means (±1 SE). Similar letters indicate a non-significant difference between communities, whereas similar numbers indicate a non-significant difference between competition treatments in the shrub community.
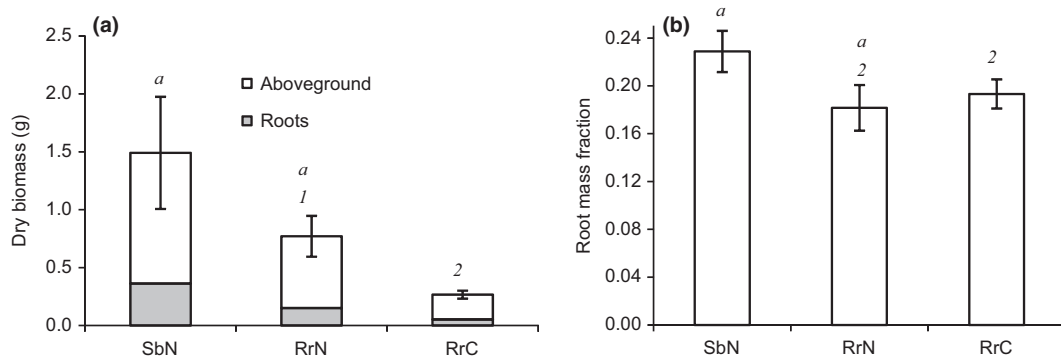

Fig. 5. Dry biomass **(a)** and root mass fraction **(b)** of seedlings of *R. robusta* 268 d after transplantation into competition exclusion plots in the grass community (SbN), competition exclusion plots in the shrub community (RrN), and in competition plots in the shrub community (RrC). Data are means (±1 SE). Similar letters indicate a non-significant difference between communities, whereas similar numbers indicate a non-significant difference between competition treatments in the shrub community.

count and biomass between the seedlings grown in soils from different communities (one-way ANOVA, $F_{(1,8)} = 1.85$, $P = 0.063$ and $F_{(1,8)} = 4.65$, $P = 0.068$, respectively).

However, seedlings grown in the grass community were significantly taller (one-way ANOVA, $F_{(1,8)} = 22.33$, $P = 0.002$) than those grown in their own community soil

type (Figs 4 and 5). There was no significant difference in the root mass fraction of *R. robusta* seedlings between the two communities ($F_{(1,8)} = 3.18$, $P = 0.118$) or between competition treatments in the shrub community ($F_{(1,8)} = 0.26$, $P = 0.062$; Fig. 5).

Discussion

Establishment of *S. brevifolia* and *R. robusta* seedlings

Results on the establishment of seedlings of the grass *S. brevifolia* were inconclusive with respect to the influence of root competition from adult vegetation or the influence of soils, since all except one seedling died early in the experiment irrespective of treatment. While further tests on the hypothesis are needed, the potential for below-ground resource competition between grass seedlings and mature leaf-succulent shrubs exists, given the dense mesh of shallow roots that characterize the root system of leaf-succulent shrubs in general (Esler et al. 1999; Carrick 2001; Shiponeni et al. 2011). Root excavations and root biomass studies for *R. robusta* shrubs revealed that more than 90% of the root biomass is found in the top 20 cm of the soil, spreading horizontally up to more than 1 m away (Carrick 2003; February et al. 2011; Shiponeni et al. 2011). We could not rule out the hypothesis that *S. brevifolia* seedlings would perform better when grown in soils from their own community rather than in those from the *R. robusta* community. However, in a previous study, variations in underlying soil properties across community gradients of grasslands and succulent shrublands, explained $\leq$ 15% of the variation in vegetation distribution (Shiponeni 2007). In the multivariate ordination and correlation analysis, soil depth and sand content were weakly positively correlated with *S. brevifolia* and negatively correlated with *R. robusta*, while organic matter and phosphorus were negatively correlated with *S. brevifolia* (Shiponeni 2007).

When *R. robusta* seedlings were grown together with mature *S. brevifolia* plants, competitive effects were strong enough to cause high mortality of *R. robusta* seedlings. This effectively prevented them from successfully colonizing grass communities and provides support for the competitive exclusion model (Hardin 1960; Brown 1971; Armstrong & McGehee 1980). Grass tussocks possess an extensive fibrous root system and are capable of taking up more available soil resources and successfully competing against seedlings of low woody plants (Kochy & Wilson 2000). Established *R. robusta* vegetation, on the other hand, had no impact on the survival of seedlings of its own species, but the seedlings exposed to root competition were significantly smaller, and the average number of leaves per seedling was three times less than when not exposed to root competition. The impact of intra-specific competition

on seedling growth, rather than survival, has been reported in the literature (Fenner 1978; Howe & Snaydon 1986; Aguilera & Lauenroth 1993), and although seedlings may remain stunted, their survival has an important ecological influence on the regeneration of *R. robusta* communities in the study area.

Soil depth, soil texture and organic content are among the commonly reported soil variables that affect local vegetation patterns by influencing local soil moisture and nutrient regimes in arid environments where water is limiting (Bowers & Lowe 1986; El-Ghani 2000; Buxbaum & Vanderbilt 2007). Our results show that in the absence of competition, *R. robusta* seedlings established successfully in the grass community, with no difference in survival, number of leaves or biomass between seedlings grown in the grass community and those grown in the shrub community. This suggests that any differences in such soil properties are less important than competition in structuring these plant communities. While leaf-succulent shrubs may occur more frequently than C_4 grasses on shallow, loamy and fertile soils in the region (Lloyd 1989; Carrick 2001), our results show that the failure of leaf-succulent shrubs to colonize grass communities at the ecotone appears to be a result of competitive interactions between these growth forms. The importance of competition in controlling the abundance of Succulent Karoo species (two *Ruschia* spp.) was reported at the boundary between the Fynbos and Succulent Karoo biome, where the abiotic environment was considered unimportant in limiting the establishment and survival of Succulent Karoo species (Lechmere-Oertel & Cowling 2001; Agenbag et al. 2004). It was, surprising that *R. robusta* seedlings were significantly taller when grown in the grass community than when grown in the shrub community, particularly since light conditions are not likely to vary between open sites within the two communities. This anomalous trend was, however, also found in the Lechmere-Oertel & Cowling (2001) study, where the two *Ruschia* spp. (Succulent Karoo seedlings) accumulated more biomass when grown in coarser-textured, nutrient-poor soils in comparison with finer-textured, nutrient-rich soils.

Many factors, particularly drought and photosynthetic pathway, might have contributed to the high mortality of *S. brevifolia* seedlings, although this effect did not have the same impact on *R. robusta* seedlings. The start of the experiment coincided with an exceptionally wet April, but rainfall in the months of May and June was relatively low and no rain fell in the winter period July–September (Fig. 1). Several comparative seedling experimental studies have revealed a remarkable ability of various *Ruschia* spp., including *R. robusta*, to survive extreme drought conditions. In these experiments, the majority of leaf-succulent seedlings survived long after all seedlings of non-succulent

species had died (Esler & Phillips 1994; Carrick 2001; Lechmere-Oertel & Cowling 2001; Hoffman et al. 2009). The mortality of all grass seedlings in both communities, irrespective of competition treatments, suggested that suitable environmental conditions are critical for the establishment of this species. Our results, therefore, provide insights into the relative survivorship for *S. brevifolia* and *R. robusta* seedlings. It remains to be tested if the C_4 photosynthetic pathway of this grass species may favour establishment during summer, while the facultatively CAM shrub may grow whenever soil moisture is available.

Compared to *R. robusta*, which seems to establish better as seedlings, adult *S. brevifolia* plants appear to be more competitive, as demonstrated in a nearest-neighbour analysis study at the ecotone, where *S. brevifolia* had relatively stronger competitive impacts on established *R. robusta* individuals (Shiponeni et al. 2011). The importance of trade-offs between traits or performance on different niche axes in facilitating co-existence of species has been highlighted (Silvertown 2004). A trade-off between high drought tolerance (succulent shrub strategy) and strong competition (grass strategy) may thus be one of the mechanisms facilitating the co-existence of grass and succulent shrubs at the ecotone. The notion that plants in arid environments concentrate their energy on surviving water deficits, rather than on competitive interactions with neighbouring plants (Medinski et al. 2010) may be supported in the case of *R. robusta,* but it may be too simplistic, indistinguishable in practice and not noted as a general trend (e.g the strongly competitive adult *S. brevifolia*).

Implications for ecotone dynamics

Ecotonal species are at the limit of their distribution range, in this case as set by the climatic boundary between the predominantly summer rainfall Nama Karoo and predominantly winter rainfall Succulent Karoo biomes. The vegetation is thus likely to be sensitive to directional change or variations in environmental conditions at different temporal scales (Holland 1988; Gosz 1993; Neilson 1993) acting upon their competitive abilities. The complexity of competitive interactions across temporal and spatial environmental gradients has been extensively debated at a conceptual level (Grime 1977; Welden & Slauson 1986; Tilman 1987; Campbell & Grime 1992; Goldberg & Novoplansky 1997; Craine 2005). It is further argued that in years of high rainfall, such as during El Nino events, successful seedling establishment might occur irrespective of the competitive regime (e.g. Marone et al. 2000). However, even in communities where *S. brevifolia* and *R. robusta* co-occur, the existence of inter-specific competitive interactions was supported, with relatively stronger impacts on adult *R. robusta* (Shiponeni et al. 2011).

Traits such as the very high number of seeds produced by *R. robusta,* and the extreme drought tolerance of its seedlings (Esler & Phillips 1994; Carrick 2001; Lechmere-Oertel & Cowling 2001; Hoffman et al. 2009) may, however, lead to far higher numbers of *R. robusta* seedlings establishing successfully than those of *S. brevifolia*. This might not only compensate for its relatively poor competitive ability, but might also promote its co-existence in the area. This suggests that while competition largely contributes to this complex pattern of segregation and aggregation of species, characterizing community assembly at the ecotone, it is not the only mechanism. Several hypotheses suggest that the importance of facilitation among plants may increase with increasing environmental harshness, and there is increasing evidence to suggest the importance of facilitation in structuring semi-arid plant communities (Bertness & Callaway 1994; Carrick 2003; Anthelme et al. 2007; Anthelme & Michalet 2009). The possibility of facilitation through protection from herbivores has been recognized in the succulent Karoo, but no evidence has been found under the moderate browsing intensities of commercial rangelands (Milton 1994; Todd 2001). Both *Stipagrostis* and *Ruschia* are palatable to livestock, so grazing is not likely to have an obvious selective effect, especially because both grass and shrub communities at the ecotone are equally exposed to the moderate grazing intensities of commercial farming systems.

Competition in arid and semi-arid environments has been considered relatively unimportant in structuring arid environments (e.g. Grime 1977), but more recently, below-ground competition in particular has received considerable attention (e.g. Tilman 1987; Goldberg & Novoplansky 1997). Cowling & Hilton-Taylor (1999) and Esler et al. (1999) hold a similar view, that competition between plants had a negligible influence on the vegetation of the Succulent Karoo biome, despite evidence to the contrary (Cunliffe et al. 1990; Yeaton & Esler 1990; Esler & Cowling 1993). Our study presents an example of where the fundamental niche for *R. robusta* may be differerent from its realized niche, as a result of competitive interactions with *S. brevifolia*.

Acknowledgements

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