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Original article

## Belowground zone of influence in a tussock grass species

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### ABSTRACT

Belowground plant competition is strong and mediated by resource depletion as well as by high variety of exudates. Both factors contribute to active root segregation, affecting neighbours' growth. In field and greenhouse experiments we investigated the belowground zone of influence of *Stipa tenacissima*, a tussock-forming grass which is the dominant species in many semiarid communities of the western Mediterranean Basin. Sometimes tussocks show a fringe nearly devoid of annual plants, most likely caused by competition or interference. Fringe size was a function of water availability, so that the more water available the smaller the fringe and *vice-versa*. Aboveground mass of annual plants was higher in gaps than in the fringe, but root mass was higher in the fringe. More species emerged in soils from gaps than in soils from the fringe, and productivity was ten times higher in soils from gaps than in soils from the fringe. Growth of barley plants was inhibited in the vicinity of *S. tenacissima* tussocks. *S. tenacissima* produced a belowground zone of influence around the tussock through resource depletion, particularly water, but also likely through root exudates. Both mechanisms might inhibit the establishment of other annual and grass species within the fringe. Fringe area has important effects for plant establishment, influencing population and community dynamics in these semiarid environments.

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### 1. Introduction

Competition affects the spatial distribution of individuals and species, playing an important role in structuring plant populations and communities, but our mechanistic understanding of competitive interactions is still poor (Cahill et al., 2005). Belowground resource competition is strong and has been associated with spatial segregation of roots (Brisson and Reynolds, 1997; Casper and Jackson, 1997) as plants alter their root production in the presence of other plants (Campbell and Grime, 1989; Friend et al., 1990; Campbell et al., 1991; de Kroon and Hutchings, 1995; Gersani et al., 1998). Roots are able to either avoid other roots (Mahall and Callaway, 1991; Schenk, 2006) or proliferate in their presence (Gersani et al., 2001), and interfere or inhibit growth of neighbours (Bais et al., 2003; Bertin et al., 2007). These effects may be mediated through an enormous variety of root exudates (Walker et al., 2003). In addition to evidence suggesting that secondary compounds contribute to active root segregation (Mahall and Callaway, 1991, 1992; Perry et al., 2005) it also shows that they also affect neighbours' growth (Bertin et al., 2007). It has been shown, for instance,

how the grass *Agropyron desertorum* inhibits growth of the shrub *Artemisia tridentata* (Caldwell et al., 1991) and the grass *Elymus lanceolatus* (Huber-Sannwald et al., 1998), and Mahall and Callaway (1991) documented similar processes between *Ambrosia dumosa* and *Larrea tridentata*. It has also been reported how the success of *Centaurea maculosa* (spotted knapweed), an invasive species in North America, is based on the secretion of catechin in roots, a compound that induces resistance to bacterial pathogens but also acts as phytotoxin (Prithiviraj et al., 2007). Similarly, fescue (*Festuca* spp.) displaces neighbouring species by depositing large quantities of phytotoxic root exudates, which interfere with root development of neighbouring plants (Bertin et al., 2007). This evidences that interference at the fine-root level is an influential component of a species' competitive success (Caldwell et al., 1996).

Root interactions are, indeed, essential to determine competitive success, particularly in patchy environments where the better-suited species will occupy the most fertile microsites (Campbell and Grime, 1989); or in resource-limited environments where species need to exploit larger volumes of soil when foraging. It is thus important to know the root zone of influence, or the area over which a plant controls its underground environment, to be able to predict and model competitive interactions. Our knowledge, however, on the size and shape of belowground zones of influence is still limited (Casper et al., 2003). Overall, plants are able to induce

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strong patterning in soil properties (Vinton and Burke, 1995), like perennial tussock grasses in arid environments, which create strong soil spatial patterns related to root foraging (Jackson and Caldwell, 1993). Production of secondary metabolites and root exudates is enhanced in stressful environments, which is why evidence for root segregation has emerged mainly from arid and semiarid systems (Schenk et al., 1999). In addition, secondary compounds produced by roots have often toxic effects on other roots, interfering with the growth of neighbours (Bertin et al., 2007). All these processes may affect plant interactions and impact both community and ecosystem dynamics.

Plant communities on hill slopes around the Tabernas basin (Almería, Spain) are often dominated by esparto grass, *S. tenacissima* L., a tussock-forming perennial C<sub>3</sub> species. Gaps between tussocks are occupied by scattered shrubs and a community of annual species whose density and composition change from year to year. In recently abandoned croplands it is possible to see a fringe void of annuals around each *S. tenacissima* tussock, suggesting exclusion mechanisms. Here we tested whether the absence of most annual species around *S. tenacissima* tussocks may be caused by resource competition and interference, most probably by allelopathy, and its significance for community dynamics. We hypothesised that 1) annuals do not establish in the fringe around the plant because of strong competition for water by *S. tenacissima*, whose roots dominate superficial soil layers around the tussock; and 2) seeds of annual and perennial species would be available at all sites, maybe in unequal proportions per species, but prevented from germination by interference from *S. tenacissima* assuming equal seed predation in fringes and gaps.

## 2. Methods

### 2.1. Field site and species

The field site was located at the Ramblilla de Genaro, a small valley near Tabernas, Almería Province, Spain (37°01' N, 2°25' W, 350 m elevation) in the northern foothills of the Sierra Alhamilla range, 20 km north of Almería city. The local climate is Mediterranean semiarid with a mean annual precipitation of 242 mm and a pronounced dry season from June to September during which there is almost no rain most years. Mean annual temperature in Tabernas (490 m elevation, 3 km to the east) is 17.9 °C with mean maxima of 10.7 °C in January and 34.7 °C in August. Soil is a calcic regosol with pH close to neutral. Other characteristics of the site and climate have been described elsewhere (Pugnaire et al., 2004).

The local plant community is patchy, covering less than 30% of soil surface. *S. tenacissima*, a perennial tussock grass, is the dominant species representing up to 60% of total plant cover (Pugnaire et al., 2004). Interspersed in the grassland are several shrub species such as *Retama sphaerocarpa* ( $6 \pm 1.05\%$  cover; mean  $\pm$  coefficient of variation, CV) and salt-tolerant species such as *Salsola oppositifolia* ( $9.9 \pm 2.56\%$  cover, mean  $\pm$  CV). Presence of salt-tolerant species has been associated with high soil salinity.

*S. tenacissima* L. is a long-lived grass which forms tussocks by aggregation of tillers (Armas, 2004). Plant growth stops during the summer, when water deficit reaches a maximum. However, the arrested development of *S. tenacissima* leaves is not due to summer dormancy because they respond opportunistically within days to pulses of water (Pugnaire et al., 1996). Root-to-shoot ratio is low, roots spread superficially and reach up to 0.5 m deep under the tussock centre (Armas, 2004). Like other species in the genus (Gurevitch, 1986), *S. tenacissima* often occurs on rocky outcrops. *S. tenacissima* communities form one of the most representative vegetation types in the semiarid region of the western Mediterranean basin (Le Houérou, 2001).

### 2.2. Sampling procedures

In October 1999, 20 mature tussocks, roughly equal in size, were randomly selected, 10 in a relatively concave area and 10 few metres apart in a relatively convex area, expecting differences in soil humidity. Tussocks were at least 2 m apart from each other and the fringe void of other plants was generally evident (Appendix A). Duplicate soil cores (311 cm<sup>3</sup>, 10 cm depth) were collected close to the tussock edge always from the W aspect. A soil core from each duplicate was weighed in the field immediately after collection, dried at 70 °C for 24 h and weighed again in the laboratory to calculate gravimetric water content. All soil samples were placed in paper bags and transported to the laboratory for further analyses. Soils from one set were passed through a 2 mm sieve and roots were separated from the soil. The proportions of the clay and silt fractions were determined by mass loss after sieving (through a 0.05 mm mesh) soil samples from which organic matter had previously been removed by combustion (Porta et al., 1986). Subsamples of each soil, passed through a 2 mm sieve, were finely ground for nutrient analysis. Total phosphorus (P) concentration was determined by emission spectrometry in inductively coupled plasma (Perkin Elmer ICP5500, USA) after samples were digested in a mixture of HNO<sub>3</sub> and HClO<sub>4</sub> in a warm sand bath at ambient pressure. Total Nitrogen (N) was determined by Kjeldahl analysis with SeSO<sub>4</sub>–K<sub>2</sub>SO<sub>4</sub> as catalyst in a Tecator 20 digestion system and a Kjelttec-auto 1030 analyser (Tecator, Sweden).

Roots were separated from soil particles by flotation after shaking for 1 h with a dispersal agent (sodium hexametaphosphate). Roots were then sorted out, dried at 70 °C for 24 h and weighed. Data were expressed on an area basis (g of roots per square metre of soil surface).

The width of the edge void of plants around each tussock was measured in all four aspects, and its area calculated as that of a circular crown. We also measured mid-day leaf water potential (Koide et al., 1989) of the youngest, fully developed leaf in a randomly selected tiller from each *S. tenacissima* tussock in concave (relatively drier) and convex (relatively wetter) soils using a pressure chamber (Skye Instruments, UK).

In our field site we did not find any *S. tenacissima* tussock growing with other perennial species within the mean fringe area or inside the tussock. Thus, we only sampled the community of annual species present at the edge of the 10 tussocks in the concave area (W aspect) and in 10 nearest gaps (1–2 m apart) at the peak of biomass production in April 2000 using 10 × 10 cm quadrats. The community of annuals in this environment is poorly developed and plant height generally did not exceed 10 cm. Within each quadrat we collected all the aboveground plant parts which were dried in a ventilated oven at 70 °C for 48 h and weighed.

### 2.3. Sowing experiments

In order to assess the effects of *S. tenacissima* roots on annuals, in November 1999 we sowed 20 barley seeds near each tussock in ~2 cm deep holes forming parallel rows at 10, 30 and 100 cm away from the tussock edge towards the gaps. Barley plants, protected from herbivory by mesh cages, were harvested 2 months later, dried in a ventilated oven at 70 °C for 48 h and weighed.

To check for persistent effects of *S. tenacissima* on the soil, we took 15 × 10 cm undisturbed soil blocks 3 cm deep from the fringe of another set of 10 tussocks and 10 from neighbouring gaps. Soil blocks were placed on trays and brought to a growth chamber with 25/18 °C day/night temperature regime, where they were watered regularly. Radiation was provided by 1000 W metal-halide lamps supplemented with 100 W incandescent lamps, reaching about 700 μmol. At the end of February, after three months in the growth

chamber individual plants were identified to the species level and harvested, and dry mass obtained as above.

#### 2.4. Data analyses

Means of soil and plant traits, water potential and number of species in gap and fringe soils as well as in convex and concave areas were compared by one-way ANOVA to a significance level of 0.05. Differences in biomass of barley plants sown at increasing distances of tussocks from convex and concave areas were analyzed by factorial ANOVA. Plant mass data were log-transformed to normalize their distribution. We checked the homogeneity of variances using Levene's test. Homocedasticity was met in all cases except for the statistical interaction between distance from tussock and convex/concave areas. As ANOVA analyses are quite robust to slight unequal variances (Kikvidze and Moya-Laraño, 2008), homocedasticity was met for main effects, and the result from the interaction between factors was not significant, we maintained the factorial ANOVA. Post-hoc differences were tested with Fisher LSD test. Data were analyzed with Statistica 9.0 software (Statsoft Inc., Oklahoma, USA). Results are presented as mean values  $\pm 1$  SE throughout the text.

### 3. Results

The physical and chemical characteristics of soils were similar in fringes and gaps (Table 1) which only differed in soil moisture content, being slightly higher in the fringe. There were no differences between gaps and fringes in N, P or OM, but there were huge differences in root mass and in the aboveground mass of annual plants between the two positions (Table 1) with opposite trends; while root mass was 9 times higher in fringes than in gaps, mass of annuals was 23 times higher in gaps than in fringes.

Water potential of *S. tenacissima* individuals in the concave, relatively moister soil was significantly higher than in the convex, relatively drier soil (Table 2). The fringe devoid of annual plants around the tussocks was larger and more apparent in convex than in concave areas, where the fringe could not often be told apart from gaps. There was a negative linear relationship between fringe area and *S. tenacissima* leaf water potential, suggesting that fringe size was a function of water availability, so that the more water available the smaller the fringe (Fig. 1).

Size of barley plants sown in the concave area with moister soils was higher than in the convex area with drier soils (Table 2,  $F_{1,51} = 5.02$ ,  $P = 0.03$ ). The seeding experiment also showed that barley mass depended on the distance to the tussock, increasing with distance (Table 3,  $F_{2,51} = 4.17$ ,  $P = 0.02$ ). Barley mass was also different between relatively moister and drier sites in the proximity of the tussock (10 cm from the tussock edge) and outside the fringe (i.e., 100 cm from the tussock edge,  $P = 0.09$ ), but not at intermediate distances within the fringe.

The blocks of soil kept in the growth chamber showed significant differences in species composition and biomass production. More species emerged in soils from gaps than in soils from the fringe (Table 4). Dry mass production in blocks was ten times higher in soils from gaps than in soils from the fringe (Table 4);

**Table 1**  
Physical properties of soil, nutrients (N: nitrogen; P: phosphorus; OM: organic matter), total root mass, and aboveground mass of annuals in gaps and at the fringe of *S. tenacissima* tussocks. Values are mean  $\pm 1$  SE,  $n = 10$ .  $P$  values from ANOVA; significant differences noted by bold values.

	Soil moisture (% vol)	Fine soil particles (%)	N (%)	P (mg kg <sup>-1</sup> )	OM (%)	Root mass (g/m <sup>2</sup> )	Above-ground biomass (g/m <sup>2</sup> )
Gaps	5.43 $\pm$ 0.53	15.2 $\pm$ 0.7	0.091 $\pm$ 0.011	5.0 $\pm$ 0.6	0.96 $\pm$ 0.19	7.4 $\pm$ 3.3	131.7 $\pm$ 23.4
Fringe	8.85 $\pm$ 1.01	15.0 $\pm$ 1.1	0.089 $\pm$ 0.016	5.7 $\pm$ 0.9	0.77 $\pm$ 0.15	67.9 $\pm$ 25.2	5.6 $\pm$ 1.2
$P$	<b>0.01</b>	0.87	0.83	0.56	0.46	<b>0.03</b>	<b>&lt;0.001</b>

**Table 2**

Mean mid-day leaf water potential ( $\Psi_l$ ) of *S. tenacissima* tussocks, size of the fringe void of vegetation around the tussocks, and mass of barley plants sown in concave (relatively wetter) and convex (relatively drier) soils in a community of *S. tenacissima*. Values are mean  $\pm 1$  SE,  $n = 9-10$ .  $P$  values from ANOVA.

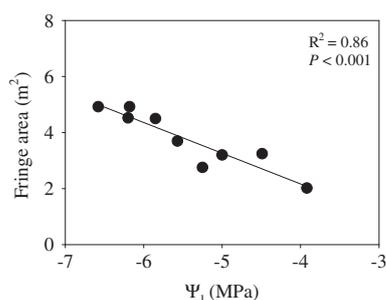
	$\Psi_l$ (MPa)	Fringe size (m <sup>2</sup> )	Barley mass (mg)
Concave	-3.39 $\pm$ 0.16	0.5 $\pm$ 0.1	5.48 $\pm$ 0.48
Convex	-5.02 $\pm$ 0.36	3.7 $\pm$ 0.3	4.15 $\pm$ 0.35
$P$	0.02	<0.001	0.03

plants that emerged from fringe soils were much smaller (Appendix A), and total biomass per species was usually lower than those emerging from gaps (Table 4). Annuals such as *Carrichtera annua*, *Reichardia tingitana*, or *Sonchus oleraceus* were completely absent in the fringe but present in gaps.

### 4. Discussion

Our results show slight or almost no differences in soil physical properties between fringe and gap microsites which, together with the scant plant community around individual tussocks, suggest that *S. tenacissima* was the cause of the fringe void of plants around tussocks. The fringe seemed to outline a zone of almost exclusive use by *S. tenacissima* where few other plant species were able to establish. Particularly excluded were graminoids like *S. capensis* but also *S. tenacissima* seedlings, and although not completely absent, growth of these and many other species was highly limited by the presence of tussocks. The large amount of *S. tenacissima* roots in the fringe, as compared with gaps, points to competition as the likely mechanism causing these areas to be devoid of other plants. A similar case occurs in New Zealand with *Hieracium pilosella* (hawkweed) which grows in patches surrounded by bare soil ('haloes'; Boswell and Espie, 1998). Boswell and Espie (1998) found that *H. pilosella* exploited moisture and nutrients in its surroundings so that soil in the halo zone was drier and relatively depleted of nutrients. The combined effects of reduced moisture and increased acidity of the soil make the immediate hawkweed environment unfavourable for the development of competing plant species (Boswell and Espie, 1998).

In our field site water is a key resource and, not surprisingly, fringe size negatively correlated to water availability, measured as *S. tenacissima* water potential. Competition seemed to be stronger under low water availability, the convex areas, leading to larger exclusion zones. On the contrary, in the relatively moister concave areas the fringe was small or non-existent. Water may have also diluted to some extent the possible allelopathic compounds exuded by the roots of *S. tenacissima*, weakening their potential detrimental effects as soil water availability increased. Overall, this supports the idea that competition for water and interference can be strong in this environment and that *S. tenacissima* is a tough competitor. Indeed, *S. tenacissima* may outcompete early colonizer shrubs, like *Cistus clusii*, in nearby abandoned croplands (Armas and Pugnaire, 2005) decreasing the diversity of perennial species.



**Fig. 1.** Linear regression between fringe area around *S. tenacissima* tussocks and mid-day water potential of *S. tenacissima* leaves.

Ramírez et al. (2009) also provided evidence of intense intraspecific competition for water and nutrients among neighbouring *S. tenacissima* tussocks in semiarid grasslands dominated by this species, suggesting that root zones of influence of *S. tenacissima* tussocks overlapped substantially in high density stands (Ramírez and Bellot, 2009; Ramírez et al., 2009). Christian and Wilson (1999) described areas which contained few native species in fields dominated by the invader grass *Agropyron cristatum*, resulting in significantly lower species richness and diversity. Growth forms most similar to *A. cristatum*, that is, C<sub>3</sub> grasses, were most likely to be excluded. Belowground competition is generally size-symmetric (Cahill, 2003), and there is evidence on how tussock grasses outcompete seedlings and species with similar root systems (Caldwell et al., 1991; Kolb and Robberecht, 1996).

In our field site *S. tenacissima* particularly excluded annual species and grasses from its surroundings and, significantly, its own seedlings. In fact, *S. tenacissima* seedlings of this and other species in the genus (Gurevicht, 1986) appear often in rocky outcrops because they do not stand competition from annuals. Our data show that competitive exclusion by adult tussocks should be considered as well. In mature *S. tenacissima* communities the fringes of different tussocks are in contact to each other, greatly decreasing the number of annuals and their size in gaps between tussocks and limiting *S. tenacissima* recruitment from seeds. Recruitment from seeds is rare and infrequent in many clonal species such as tussock grasses (Eriksson, 1992) because of competition between adults and seedlings (Bonanomi et al., 2005). In fact, the number of *S. tenacissima* plants establishing from seeds in these communities is negligible despite the high number of seeds produced (>1200 caryopses/m<sup>2</sup>; Haase et al., 1995). *S. tenacissima* tussocks, however, did not affect the presence of lichens, which were apparent in fringes with no annuals, because lichens may not significantly compete for resources with vascular plants (Pavlov et al., 1998).

Other studies have shown strong facilitative effects of *S. tenacissima* tussocks on saplings of different shrub and tree species planted within the tussock or in the grass zone of influence (Maestre et al., 2001, 2003; Gasque and García-Fayos, 2004), or

**Table 3**

Mass of barley plants sown in concave (relatively wetter) and convex (relatively drier) soils in a *S. tenacissima* community at increasing distance from the edge of the tussock. Values are mean ± 1 SE, n = 9–10. P values from post-hoc Fisher LSD test after ANOVA.

		Distance from the tussock edge (cm)		
		10	30	100
Plant mass (mg)	Concave	5.1 ± 0.9	4.9 ± 0.6	6.3 ± 0.7
	Convex	3.0 ± 0.6	4.6 ± 0.7	4.8 ± 0.4
P		0.04	ns	0.09

**Table 4**

Total number of species, mean number of species per sample, dry mass of annuals (total and biomass per species) in block-soils from the fringe around tussocks and from gaps in a community of *S. tenacissima*. Values are mean ± 1 SE, n = 10. P values from ANOVA.

	Fringe	Gaps	P value
Total number of species	7	10	–
Mean number of species	3 ± 0.4	7 ± 0.5	<0.001
Total mass (g/m <sup>2</sup> )	6.0 ± 0.6	61.9 ± 6.3	<0.001
Biomass/sp (mg)			
<i>Asterolinum linum-stellatum</i>	34.0 ± 16.0	127.1 ± 33.1	0.02
<i>Calendula tripterocarpa</i>	2.7 ± 2.7	22.5 ± 8.3	0.04
<i>Carrichtera annua</i>	–	32.0 ± 13.3	–
<i>Erodium chium</i>	22.8 ± 17.6	137.0 ± 59.0	0.08
Grasses	71.0 ± 25.6	1008.1 ± 185.1	<0.01
<i>Linaria nigricans</i>	1.3 ± 1.3	31.2 ± 10.9	0.01
<i>Lycocarpus fugax</i>	5.4 ± 5.4	5.2 ± 3.0	0.98
<i>Medicago truncatula</i>	12.2 ± 9.0	25.7 ± 17.8	0.51
<i>Reichardia tingitana</i>	–	106.6 ± 88.7	–
<i>Sonchus oleraceus</i>	–	199.8 ± 80.1	–

have shown quite different outcomes, from net positive to negative, depending on the ontogeny of the shrub species used (Soliveres et al., 2010). Such data are in sharp contrast with those reported here or, for example, in Ramírez et al. (2009). The main differences among the two groups of data depend on the experimental design. While in our case, and in Ramírez et al. (2009), the focus was on the effects on natural vegetation, grasses and annual species, the other studies assessed the effect of the grass on planted shrubs and trees. Niche differentiation between the shrubs, trees and *S. tenacissima* may be responsible. Armas and Pugnaire (2005) and Soliveres et al. (2010) showed that net competition of *S. tenacissima* on shrubs gradually decreased as shrub and grass aged, suggesting niche differentiation as evidenced in other shrub–grass steppes (Sala et al., 1989). Caldwell et al. (1996) also showed that shrub and grass roots tend to avoid each other to prevent interference at the fine-root level. Planted shrub and tree saplings had greater survival on small terracettes upslope of *S. tenacissima* tussocks or beneath the canopy of tussocks that were experimentally killed but left in the field (i.e., saplings did not suffer competition from *Stipa* tussocks) than in bare ground (Maestre et al., 2001, 2003; Gasque and García-Fayos, 2004). On slopes, *S. tenacissima* tussocks intercept runoff fluxes (Puigdefábregas, 2005) forming small terracettes that can be defined as resource islands (Puigdefábregas and Sánchez, 1996) with higher infiltration rate, water holding capacity, nutrient content and microbial activity than surrounding bare areas, and usually milder microclimatic conditions than in gaps (Bochet et al., 2000; Maestre et al., 2001; Goberna et al., 2007). Our field site is relative flat with no formation of terracettes near tussocks and in such conditions our results show that soils around tussocks, the root zone of influence, have characteristics similar to gaps and exert great control on natural vegetation.

The root zone of influence determines plant density as a function of resource availability. Species that utilize resources efficiently may particularly benefit from active root segregation because more profligate neighbouring species would not be able to take resources that were being utilized slowly (Schenk et al., 1999). A similar conclusion is supported by our sowing experiment, where barley plants had similar size at intermediate distances from the tussock in both relative wet and dry soils but tended to differ at further distances from the tussock, suggesting that competition outside the root area of influence was determined by water availability. Morgan (1997) in a similar experiment with *Themeda triandra*, a tussock grass species, found that emergence of *Rutidosia leptorrhynchoides* (Asteraceae) seedlings was greatest as distance from the grass increased (i.e., in larger gaps), but survival was restricted to gaps at least 100 cm in

diameter. He found that juvenile plants were better competitors than seedlings. Survival, growth rate and total number of inflorescences produced, however, were significantly greater in large gaps, showing again strong competition from the grass (Morgan, 1997).

The experiment with soil blocks in the glasshouse showed that either there were fewer seeds in the fringe or that they did not germinate. Seeds that did germinate produced feeble plants, much smaller than plants growing in gap soil. Since plants in soil blocks were not directly exposed to *S. tenacissima* effects, and soil water availability was plentiful, competition can be ruled out. The grass might also have depleted nutrients in the fringe soil compared to gaps but our data show similar levels of N, P and OM in both soils. Finally, *S. tenacissima* might have an effect on the scant plant community in fringes via two other mechanisms: by changing the soil microbial community in such a way that plant-soil feedbacks occurred, and by allelochemical compounds produced by the grass. Both mechanisms imply an effect of root exudates on the biotic communities in the fringe.

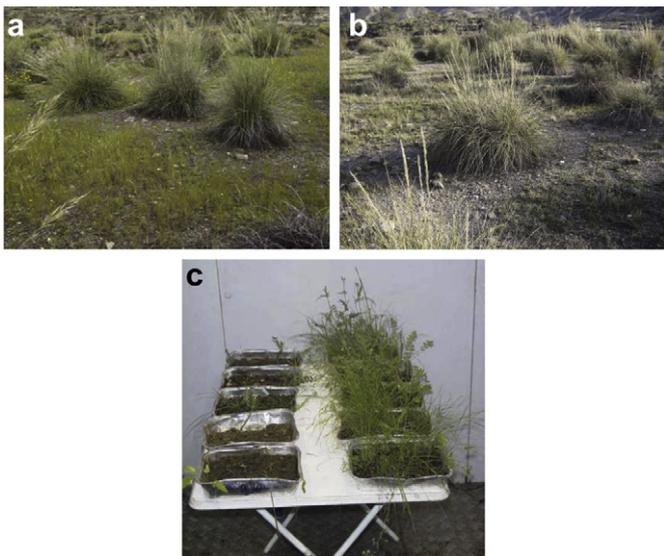
## 5. Conclusions

The presence of a fringe devoid of vegetation around *S. tenacissima* tussocks indicates an area of exclusive use by this tussock species. Competition for water and probably the production of root exudates preclude the establishment of other species, as well as its own seedlings. Knowledge about such exclusive areas is important to understand and model plant community interactions.

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## Appendices



### Appendix A.

Fringe voids of annuals around *S. tenacissima* tussocks in spring (a) when annuals merge, and in summer (b) when the community of annuals in gaps become parched. Block-soil experiment (c) in a growth chamber; blocks on the left from fringes and on the right from gaps.

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