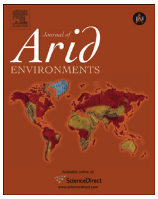
Journal of Arid Environments 102 (2014) 21–26

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv



# Field competitive equivalence between grasses differing in drought tolerance in a Patagonian semiarid steppe

L.L. Couso [a,*], F. Biganzoli [b], R.J. Fernández [a]

[a] Cátedra de Ecología, IFEVA-CONICET, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina
[b] Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina

ARTICLE INFO

*Article history:*
Received 17 April 2013
Received in revised form
4 November 2013
Accepted 7 November 2013
Available online 7 December 2013

*Keywords:*
Aggressivity
*Bromus pictus*
*Pappostipa speciosa*
Relative yield
Replacement series
Trade-off

ABSTRACT

Competition is an important interaction in systems with water limitations. Many plant species show a trade-off between stress tolerance and competitive ability. Our hypothesis was that competitive ability is higher for species less tolerant to drought. *Bromus pictus* and *Pappostipa speciosa* are two conspicuous grasses from semiarid Patagonian steppe with opposite morpho-functional characteristics. *B. pictus* is the most plastic, sheep-palatable and relatively drought-intolerant species and it is predicted to have higher aggressivity than *P. speciosa*, considering aggressivity as an index of competitive ability. A two- year field experiment was performed using a replacement series type-design with a fixed total density of two plants and three proportions of relative plant size. Two levels of water availability were evaluated. After 24 months, there was no difference in competitive ability between species (comparing aggressivity values between species, AG). However, AG was higher for plants growing in minority and lower for plants growing in majority (in relation to their neighbor size) regardless of species identity. There was no tradeoff between stress tolerance and competitive ability. Taking into account that *P. speciosa* is clearly dominant and *B. pictus* is subordinate, it seems that plant-to-plant competition would not suffice to explain population abundance within this community.

## 1. Introduction

Competitive interactions have been widely studied in ecology, both *per se* and as structuring forces, for their potential relation with distribution, abundance and characteristics of coexisting species (Clements et al., 1929; Gause, 1934; Goldberg and Barton, 1992; Trinder et al., 2013). They are related with environmental heterogeneity (Fransen et al., 2001), frequency and intensity of disturbance (Connell and Slatyer, 1977) and, above all, with the identity of limiting resources –aboveground or belowground- (Tilman, 1982) and their availability (Goldberg and Barton, 1992; Grime, 1979). Some authors state that the more scarce the limiting resources, the more intense the competition (Chapin and Shaver, 1985). In contrast, others claim that an increase in resources (e.g. water availability) results in a higher competition (Briones et al., 1998; Corcket et al., 2003; Kadmon, 1995). However, the overall evidence shows that competition is an important interaction in systems with water limitations (Fowler, 1986).

Many plant species conform to a trade-off between tolerance to stress and competitive ability (Greiner La Peyre et al., 2001; Grime, 1979; Liancourt et al., 2005; Suding et al., 2003). Grime (1979) proposed that species evolved in contrasting resource environments have opposite ecological "strategies": tolerance vs. competition. These strategies are defined by species traits. Competitive species (C-species *sensu* Grime, 1979) present a high potential growth rate when close to optimal availability of resources. Therefore, they may be intensely affected in reproduction, growth and/or survival under stress conditions. On the other hand, stress tolerant species (s- species *sensu* Grime, 1979) would be able to survive under severe stress, and even have some growth under intermediate stress, although paying a cost: the one of having a relatively low growth under non-limiting conditions. The balance between those opposite forces provides a mechanism of population coexistence.

Water availability for plants is the result of precipitation, run-off, deep percolation and evaporation, and the level of water consumption by species in the community. In this sense, water availability for a population is in part a consequence of the neighbors'

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* Corresponding author. Tel.: +54 11 4 524 8000.
*E-mail addresses:* lcouso@agro.uba.ar (L.L. Couso), biganzol@agro.uba.ar (F. Biganzoli), fernandez@agro.uba.ar (R.J. Fernández).

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http://dx.doi.org/10.1016/j.jaridenv.2013.11.001

effect on the target population (*effect* of competition, Goldberg, 1990). Otherwise, population changes in fitness due to a neighbor presence conform the *response* to competition (Goldberg, 1990). Thus, the outcome of competition depends on the intrinsic characteristic of neighbors regarding resource consumption.

We studied a semiarid steppe in western Patagonia (Argentina). Water is the main limiting resource and several grass species tolerant to drought coexist there (Golluscio et al., 2005). However, there is certain variation between species tolerance, being the extremes *Pappostipa speciosa* as the most and *Bromus pictus* as the least drought tolerant, with associated differences in morpho-functional traits (Couso and Fernández, 2012). Following Grime (1979), we asked whether the lower drought tolerance for *B. pictus* is associated with a higher competitive ability, and the higher drought tolerance for *P. speciosa* is associated with a lower competitive ability. To answer this, we performed a field experiment using a replacement-series type design (De Wit, 1960) and evaluated *B. pictus* and *P. speciosa* competitive ability (Connolly et al., 2001; Walck et al., 1999a; Weigelt and Jolliffe, 2003). With the purpose of studying the role of water availability on competitive outcome (Briones et al., 1998), we included two levels of water availability (watering and control). We worked at different time scales by analyzing the responses at 2, 12 and 24 months respectively. In order to evaluate the effect of the relative size of neighbors in the outcome of competition, we analyzed three different proportions of size. Our hypothesis, in accordance with Grime's (1979) ideas, was that competitive ability is higher for species less tolerant to drought. Water addition intensifies competition in favor of the most competitive species. Based on known physiological and morphological traits, we predicted that, *Bromus pictus* will be the species with higher competitive ability in comparison with *Pappostipa speciosa*.

## 2. Materials and methods

### 2.1. Basic design

A field trial was performed at the Patagonian steppe using a modified de Wit-replacement-series design (De Wit, 1960) design to evaluate competitive interactions. We worked with two native tussock grasses species with contrasting morpho-functional properties ("ID"): *Bromus pictus* Hook ("*Bp*"), a plastic, sheep-palatable and relatively drought-intolerant species, and *Pappostipa speciosa* (Trin. & Rupr) Romaschenko (=*Stipa speciosa*; "*Ps*"), with the opposite characteristics (Couso and Fernández, 2012; Golluscio et al., 1998; Leva et al., 2009; Semmartin et al., 2004; Soriano, 1956). Instead of using a variable plant density, as in the original de Wit's approach (De Wit, 1960), we worked with a fixed total density of 2 plants (always in pairs). We selected heterospecific pairs with one of 3 proportions of relative plant size (0.25, 0.5 and 0.75) and one (0.5) for monocultures. For every pair of plants, the relative size of the focus plant in relation to its neighbor was called "proportion of target species" or "PTS". Observations of live tiller numbers were performed 2, 12 and 24 months later in every plant. Reproductive tillers were counted after 12 months of treatment. Based on tiller data, we calculated relative yield (RY *sensu* Fowler, 1982) as a measure of the intensity of inter- vs. intraspecific competition, and aggressivity (AG) as index of competitive ability (*sensu* Snyder et al., 1994; Walck et al., 1999a,b). Species aggressivity is a useful index to evaluate subordinated and dominant species in a two-species mixture (Walck et al., 1999a; Weigelt and Jolliffe, 2003). According to our hypothesis, *Bromus pictus* was predicted to have a higher RY and higher AG than *Pappostipa speciosa*.

### 2.2. Making species comparable

As explained, we used a constant density of 2 plants per plot, using relative plant size to control for the strength of interspecific interactions. However, since the average adult plant size is different between the species, we found it necessary to use a correction factor (CF) to make them comparable. To do so, we sampled 150 individuals per species, not including seedlings or decaying plants with a large accumulation of dead material, and found out that the average number of tillers per *P. speciosa* plant tripled the average number for *B. pictus* ($Ps = 36$ vs. $Bp = 11$ on average). Thus, $CF = 3$ means that a *B. pictus* plant with 10 tillers was considered equivalent to a *P. speciosa* plant with 30 tillers. Based on the equivalent size of both plants in each heterospecific pair, we defined the corresponding PTS treatment at the beginning of the experiment.

### 2.3. Treatments and measurements

The experiment started on November 2007 at INTA's Rio Mayo experimental range (45°41′ S, 70°16′ W), within a 1-ha exclosure dating from 1973. A hundred pairs of plants (tussock grasses) were selected and labeled. Each pair was composed of plants separated by a minimum of 15 and a maximum of 25 cm at their bases. At such distance, the root system overlapped and plants competed for underground resources (Soriano et al., 1987).

There were 40 monospecific pairs (20 of each species composed of 2 plants of similar size) and 60 heterospecific pairs with differences in relative size between plants (**proportion treatments:** "PTS"). Out of heterospecific pairs, 20 were composed of 2 plants of equivalent size (0.5 *Bp*- 0.5 *Ps*), 20 were composed of a larger *P. speciosa* plant (0.25 *Bp*- 0.75 *Ps*), and 20 of a larger *B. pictus* plant (0.75 *Bp*- 0.25 *Ps*). Half of the pairs within each of these 5 configurations were randomly assigned a water availability level (**watering treatments**: addition of extra water "W+" or control without extra water "W−"; $N = 10$). Live tiller counting was repeated 2 months, 12 months and 24 months later (**time treatments:** "T", included as repeated measures). At 12 months, we also recorded reproductive tillers.

The watering treatment was applied during the Southern Hemisphere warm season (November 2007, January and November 2008, and January and November 2009), each time adding one liter of water over a 5 × 10-cm area equidistant between the members of the pair. This amounts to 20 mm, which was considered enough to wet most of the rooting profile (ca. 30 cm deep, Soriano et al., 1987). Soil is sandy and it was dry in the months of the year when watering was carried out (Golluscio et al., 2005). These conditions additional to the slow and careful watering ensured no runoff (sometimes it required dividing the water volume in two amounts applied one hour apart).

### 2.4. Analysis

To guarantee independence of results, we analyzed each pair considering only one of the plants as 'target' (leading to $N = 5$ for each combination of species, proportion, and watering level). The increase in the number of live tillers was used as a measure of plant performance. This measure has three fundamental advantages: 1) it is a non-destructive measure; 2) tillers represent the number of vegetative multiplication units (ramets, *sensu* Kays and Harper, 1974); and 3) for *B. pictus* and *P. speciosa*, tiller biomass is a highly conservative trait in relation to water availability (Couso and Fernández, 2012).

The equivalent tiller number between species was:

$$\begin{aligned} & CF^{*}Y^{I}_{Bp} = Y^{I}_{Ps} \\ & \text{and } CF = 3 \end{aligned} \tag{1}$$

with $Y^{I}_{x}$ being the initial number of tillers of specie “$x$”

After correcting by equivalent tiller number of each species, their proportion was defined as:

$$p_{Bp} + p_{Ps} = 1 \tag{2}$$

Performance (tiller production) was calculated as:

$$\text{Tiller Production}_{x} = Y^{F}_{x} - Y^{I}_{x} \tag{3}$$

with $Y^{F}_{x}$ being the final number of tillers and $Y^{I}_{x}$ the initial number of tillers of “$x$”.

Relative yield of species (RY) was calculated as:

$$RY_{Bp} = Y^{F}_{Bp-\mathrm{mix}} / \left( p_{Bp} {}^{*} Y^{F}_{Bp-\mathrm{mono}} \right) \tag{4}$$

$$RY_{Ps} = Y^{F}_{Ps-\mathrm{mix}} / \left( p_{Ps} {}^{*} Y^{F}_{Ps-\mathrm{mono}} \right) \tag{5}$$

with $Y^{F}_{x-\mathrm{mix}}$ being the final number of tillers of species “$x$” in heterospecific pairs; $Y^{F}_{x-\mathrm{mono}}$the final tiller number for species “$x$” in monocultures; $p_x$ is the initial proportion of species “$x$” in the particular mixture ($p_x$ was a fixed value at initial proportion 0.25, 0.5 or 0.75 depending on treatment).

To calculate RY of species in mixtures ($RY_{Bp}$ and $RY_{Ps}$), the monocultures (monospecific pairs) used in Eqns. (4) and (5) were not selected at random or by physical proximity, but selection was made considering similarity of initial plant size (i.e. functional equivalent). To do this, we ranked monoculture pairs classifying them by adding the initial sizes of both plants in the pair. Then, in order to calculate RY value for any heterospecific pair, we compared the most similar monoculture pair in initial size.

These RY were then used to calculate aggressiveness (AG):

$$AG_{Bp(p)} = RY_{Bp(p)} - RY_{Ps(1-p)} \tag{6}$$

$$AG_{Ps(p)} = RY_{Ps(p)} - RY_{Bp(1-p)} \tag{7}$$

An example for AG estimates: $AG_{Bp(0.25)} = RY_{Bp(0.25)} - RY_{Ps(0.75)}$. AG for *B. pictus* at initial proportion of 0.25 resulted from a comparison between RY values of *B. pictus* in 0.25 with RY values of *P. speciosa* in 0.75 (exactly the same proportion as evaluated in the field competition treatment 0.25*Bp* - 0.75*Ps*)

We used a repeated measures analysis (*lme* function from the *nlme* package, Pinheiro et al., 2013) to studied the relationship between vegetative growth (tiller production), relative yield, and aggressivity with treatments (ID, W, PTS and T). A generalized linear effect model (*glm* function from the *stats* package, R Core Team) with a binomial-distribution was used to analyze the relationship between proportion of reproductive tillers with ID, W and PTS. We used species (ID; two levels), water treatment (W+ or W−; two levels), proportion in mixed cultures (PTS; three levels) and time (T; three dates) as the fixed main effects. Initial size of the target plant was included as a covariate to control the effect of the plant size on response variables. We selected the best factor combination for varIdent option (nlme package) to correct for heteroscedasticity when necessary. We fitted the most complete model first, which included all effects and their interactions, and then simplified it by removing non-significant interactions terms until finding a minimal adequate model (Zuur et al., 2009). Statistical significance among treatments was evaluated with the *lsmeans* package (Lenth, 2013).

## 3. Results

### 3.1. Tiller production

Tiller production (difference between final and initial tiller number) was different between species but depending on time (ID × T, $p < 0.0001$; Fig. 1). There was no significant effect of either watering (W), proportion of target species (PTS), or initial size (covariate). During the first two months, both species showed similar tiller production (ID, $p = 0.667$; Fig. 1a) but since month 12 this relation changed (Fig. 1b–c). *Pappostipa speciosa* showed higher tiller production than *Bromus pictus* (ID, $p < 0.0001$). *B. pictus* showed no net tiller increase at any PTS (*Bp* mean tiller production close to 0). Conversely, *P. speciosa* had a tiller increase but that increase was similar in all PTS treatments (Fig. 1b–c).

### 3.2. Reproductive tillers (1 year)

Production of reproductive tillers was recorded on the first 12 months of treatments (Fig. 2). *B. pictus* showed a higher number of reproductive tillers relative to the total number of tillers than *P. speciosa* (ID, $p < 0.0001$; Fig. 2). The relative number of reproductive tillers showed no PTS or W effect (Fig. 2).

### 3.3. Relative yield (RY)

The effect of treatments on relative yield (RY) was a decreasing response to PTS increase (PTS, $p = 0.0026$), with no species, watering, time or initial size effect (Fig. 3). An RY of 1 reflects functional equivalence between species: the effect of one unit of any species is the same (intra-specific competition = inter-specific competition; see Eqns. (4) and (5)). When the target species was less represented than the neighbor species (PTS = 0.25; hereafter “in minority”), the effect of inter-specific competition becomes small in relation to that of intra-specific competition, thus generating an RY higher than 1 (Fig. 3b). Such a trend became more apparent after 24 months: most of the 0.75 values staying below 1, while 0.5 had values intermediate to those of the other two levels (Fig. 3c).

### 3.4. Aggressivity (AG)

Aggressivity, which compares RY between species (Eqn, 6–7), already showed PTS effects since the beginning of the experiment ($p = 0.0042$; Fig. 4). There were no W, ID, T or initial size effects. Both *B. pictus* and *P. speciosa* showed higher AG values when they grew in minority (PTS = 0.25) than when grown in “majority” (PTS = 0.75). Mean AG values for both species at 0.25 were above cero ($RY_{\mathrm{target}}$ at 0.25 > $RY_{\mathrm{neighbor}}$ at 0.75, see eqns. (6) and (7)). An AG = 0 is indicative of similar competitive ability of both species (when growing together). Thus, our AG results suggest that both species improve their competitive ability when grown in minority (at 0.25) in comparison with neighbor proportion. *P. speciosa* was dominant when grown beside *B. pictus* in higher proportions (0.25 Ps − 0.75 Bp) and *B. pictus* is dominant in the opposite case (0.75 *Ps* − 0.25 *Bp*). However, the *Bp* effect on *Ps* when $PTS_{Bp} = 0.25$ is larger than the *Ps* effect on *Bp* when $PTS_{Ps} = 0.25$ (compares the negative values of *Ps* with the less negative values for *Bp* in PTS 0.75).

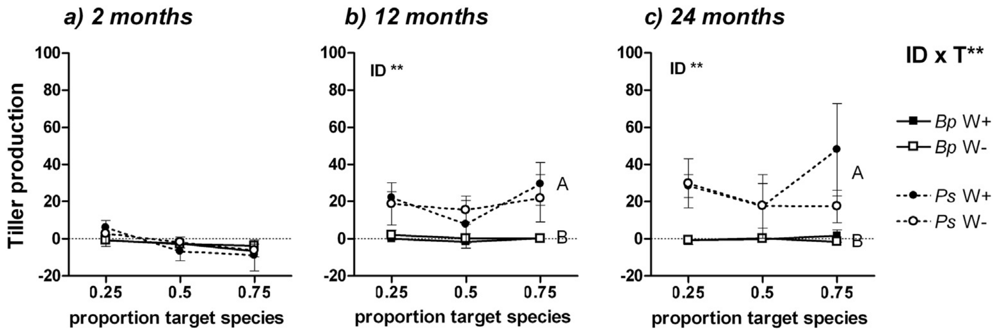

**Fig. 1.** Tiller production (Eqn. (3), uncorrected) of *Bromus pictus* (*Bp*-squares) and *Pappostipa speciosa* (*Ps*-circles) in mixtures for 3 proportions of target species (PTS), with watering treatment (W+; control: W−) at three different times (T). a) 2 months b) 12 months. c) 24 months. Differences in capital letters show differences between species identity (ID). $^{**}p < 0.001$.

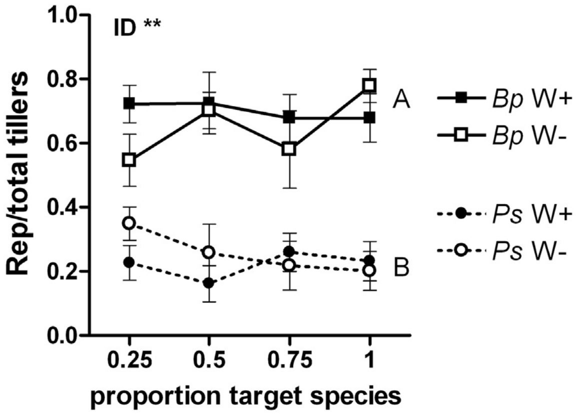

**Fig. 2.** Relative reproductive tillers (Reproductive tillers/total tillers) at 12 months of *Bromus pictus* (*Bp*-squares) and *Pappostipa speciosa* (*Ps*-circles) in mixtures for 3 proportions of target species (PTS) and with watering treatment (W+; control: W−). Differences in capital letters show differences between species identity (ID). $^{**}p < 0.001$.

## 4. Discussion

There was no difference in aggressivity (AG) between species, openly contradicting our hypothesis: *Pappostipa speciosa* and *Bromus pictus* responded in similar ways. They showed similar increases in competitive ability when each of them was in minority (PTS = 0.25 in Fig. 4), that is, when faced with a larger heterospecific neighbor. In other words, what mattered most for a target plant was not the identity of its neighbors but the pressure they imposed upon the pool of available resources (as observed for nutrients and light, Bengtsson et al., 1994). Somehow, when in minority, each species tended to overcompete its neighbor, and both species mirrored each other in this respect (shown by their overlap on Fig. 4). It follows that the relative weight of inter- and intra-specific competition (Eqns. (4) and (5)) varied with PTS (Fig. 3), the latter being larger for the species in minority and smaller for the species in majority. This would explain why a mainly 'alien' neighborhood is less aggressive for the species in minority.

Experimental approaches for the study of competition and associated indexes have been widely criticized (Goldberg and Scheiner, 1993; Jolliffe, 2000). Our approach, though, overcomes several disadvantages: we worked with established undisturbed plants in their natural field background, under two water supply conditions, and monitored their short to long-term responses. In particular for replacement-series experiments, an important criticism has been ignoring differences in size between plants of the competing species (Connolly et al., 2001). The species behaved in a similar functional way when faced with competing neighbors, as shown by their overlap in Figs. 3 and 4. Embedded in such responses, however, is a correction for tiller number (CF = 3; see Methods). This means that each *B. pictus* tiller behaved in a similar way in terms of resource use than three *P. speciosa* tillers (i.e. that our CF somewhat reflected functional equivalence). Indeed, previous work showed that the ratio between average tiller size for these species is not far from 3 (2.11 ± 0.02 field measures by Graff, 2009; 5.39 ± 0.05 glasshouse measures, Couso and Fernández, 2012).

Fig. 5 summarizes our results on the type of plot proposed by Williams and McCarthy (2001) for the likely outcome of interactions between species based on their RY values. There, the 1:1, diagonal line represents total functional equivalence between

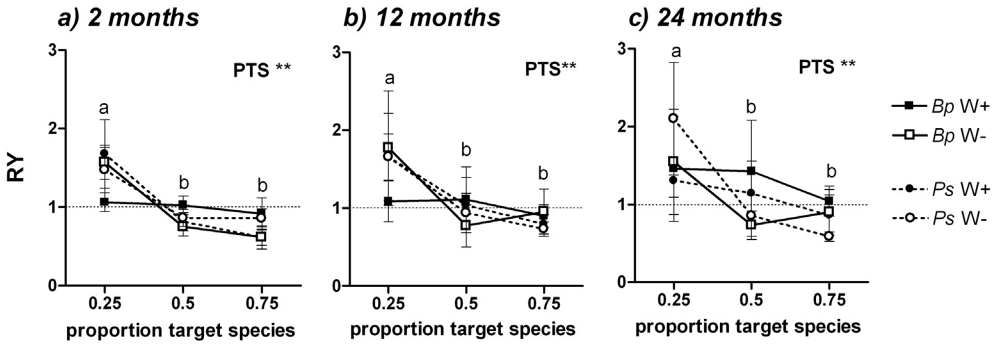

**Fig. 3.** Relative yield (RY; Eqns. (4) and (5)) of *Bromus pictus* (*Bp*-squares) and *Pappostipa speciosa* (*Ps*-circles) in mixtures for 3 proportions of target species (PTS), with watering treatment (W+; control: W−) at three different times (T). a) 2 months b) 12 months. c) 24 months. Differences in lowercase letters show differences among PTS. $^{**}p < 0.001$.

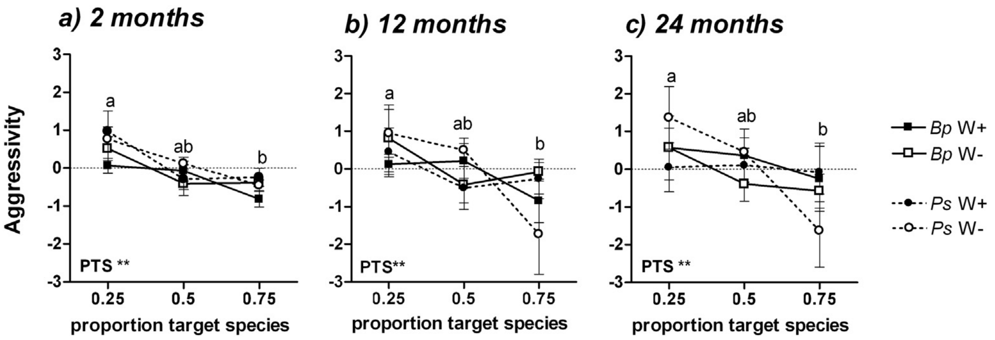

**Fig. 4.** Aggressivity (AG; Eqns. 6–7) of *Bromus pictus* (*Bp*-squares) and *Pappostipa speciosa* (*Ps*-circles) in mixtures for 3 proportions of target species (PTS), with watering treatment (W+; control: W−) at three different times (T). a) 2 months b) 12 months. c) 24 months. Differences in lowercase letters show differences among PTS. $^{**}p < 0.001$.

species (had we ignored the importance of this difference, had we assumed CF = 1, all points would have fallen above the diagonal in Fig. 5. *Ps* always disadvantaged). In agreement with our main results, the species in minority would suppress the other (unshaded areas). This was independent of the watering treatment. However, water availability did change the interaction outcome for plants of equivalent size: *Bp* was facilitated by *Ps* when the pair was watered (light shade area), but when not watered there was mutual suppression (dark shade area). Taken together, these results generate the following hypothesis: Any asymmetrical heterospecific pair of plants will, in a first stage, generate a pair of equivalent plants, and what happens next will depend on water availability: if above average, it will promote stable coexistence, but under drought conditions this would not be possible and both species would become locally extinct by mutual suppression. Our tiller production data (Fig. 1c) suggest that these changes would take observations for more than two years to be detected.

We worked with two species of known morpho-functional traits and drought tolerance that pointed towards functional differences along the S–C axis of Grime's strategies. Nonetheless, the presumed drought-sensitive species (C), was as competitive as the presumed tolerant one (S). In other words, when we tried to apply this classification, proposed for species in different communities, to species in the same community, there was no tradeoff between stress tolerance and competitiveness. Taking into account that one of these species is clearly dominant (*Ps*), and the other is subordinate (*Bp*), it seems that plant-to-plant competition would not suffice to explain population abundance within this community. Thus, it could be hypothesized that population control is exerted by some factor/s at a larger scale, such as inter-annual precipitation, operating on reproduction, recruitment or survival.

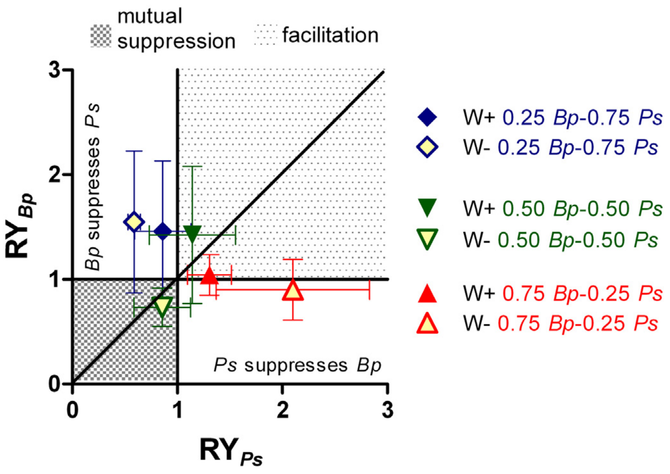

**Fig. 5.** Possible outcome of interactions at 24 months between *Pappostipa speciosa* and *Bromus pictus*, following Williams and McCarthy (2001). Symbols are $RY_{Bs}$ vs $RY_{Ps}$ values for the six treatments with their standard errors. **Treatments**. *Proportion factor* (3 levels): 0.25 – 0.75, 0.50 for both species and 0.75–0.25. *Watering factor* (2 levels): with extra water (W+) and without extra water (W−). **Six areas**: 1) Values under 1:1 line represent an advantage for *X*-axis species. 2) Values over the line show an advantage for *Y*-axis species. 3) $RY_{X\text{-axis}}>1$ and $RY_{Y\text{-axis}}<1$ show an advantage for species in *X* axis. 4) $RY_{Y\text{-axis}}>1$ and $RY_{X\text{-axis}}<1$ show an advantage for species in *Y* axis. 5) Mutual suppression (striped area): the interaction is negative for both species at a level where the persistence for any of two species in the mix is impossible. 6) Facilitation (dotted area): both species derive an advantage growing together rather than in the mix (RY > 1).

## Acknowledgments

We thank Pamela Graff, Esteban Fernández and Luciana Pizzorno for their help and support. Public funds from Argentina were provided by ANPCyT, CONICET and Universidad de Buenos Aires.

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