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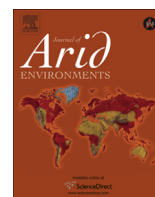
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Short communication

Early competition between the exotic herb *Rumex acetosella* and two native tussock grasses with different palatability and water stress tolerance

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ABSTRACT

Semiarid grasslands in NW Patagonia (Argentina) are dominated by *Festuca pallescens* and *Pappostipa speciosa*, two native tussock grasses that differ in water stress tolerance and in palatability to livestock. Both species regenerate in gap microsites invaded by the exotic herb *Rumex acetosella*. We performed a greenhouse experiment to study the effect of *Rumex* competition on early growth of the dominant tussock-grasses. In February 2008 we used about 4-month-old seedlings to establish competition treatments that simulated a dry or wet summer. Competition among grasses was also quantified to relativize the effect of *Rumex* competition on each grass species. *Rumex* seedlings had a negative impact on grass seedlings, but it was not greater than that produced by any co-dominant grass. Grass species did not differ in their sensitivity to competition by *Rumex* or to water stress. In dry conditions, there was an intense underground competition between grass species, but there was no evidence of underground competition from *Rumex*. The low competitive ability of *Rumex* under water stress may indicate that its invasive potential from a seedling stage would be limited by the aridity of the environment. Moreover, the high bud production of *Rumex* seedlings suggests an early contribution to the soil bud bank, a key eco-biologic trait of this invasive species. Therefore, the estimation of the bud bank abundance and the study of how vegetative regeneration may be interfering grass recruitment should be considered in future research.

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1. Introduction

For over a century, livestock production has been the main economic activity of semiarid temperate Patagonian grasslands (Argentina), and continues to be sustained by natural vegetation (Golluscio et al., 1998). Many sites with a long grazing history and/or high domestic animal loads have become degraded. High and selective grazing pressure decreases the competitive ability of over-defoliated plants (Gittins et al., 2011; Golluscio et al., 1998) thus favoring the replacement of palatable species with unpalatable species. Nevertheless, unpalatable grass species could be disadvantaged in absence of grazing since they are less competitive than palatable grass species (Moretto and Distel, 1997), which is in agreement with the hypothesis that palatability and competitive ability are positively correlated (Crawley, 1990).

Many species from semiarid environments possess physical characteristics that confer low palatability and high tolerance to drought (Grime, 1979; Moreno et al., 2010). Furthermore, according to the trade-off among the plant primary strategies (Grime, 1979), it is expected that better adaptation to stress could decrease competitive ability. The matrix of northwestern Patagonia's grasslands is dominated by *Festuca pallescens* (hereafter *Festuca*) and *Pappostipa speciosa* (ex *Stipa speciosa*; hereafter *Pappostipa*), two perennial native tussock-grasses that differ in palatability for livestock and in water stress tolerance. The former is a high value forage species that dominates at higher altitudes than the second species, an unpalatable grass (Anchorena and Cingolani, 2002; Velasco and Siffredi, 2009). This elevational change creates an environmental gradient in which *Pappostipa* inhabits the warmer and drier areas, reflecting higher tolerance to water stress than *Festuca* (Fernández et al., 2006). These and other differences in morpho-physiological traits could influence the species' vulnerability to environmental stress and disturbances during early development stages (Franzese and Ghermandi, 2012a). Such

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vulnerability could also influence the outcome of inter-specific interactions during the recruitment phase.

In western Patagonian grasslands, competition for water plays a crucial role in the establishment of native grasses (Aguilar et al., 1992; Bertiller et al., 1996; Defossé et al., 1997). Dominant grasses recruit in grassland gaps (inter-tussock areas), which are microsites with low competitive pressure (Aguilar et al., 1992; Defossé et al., 1997). However, gaps can experience more extreme microclimatic conditions than the surrounding matrix or be invaded by exotic species, factors that may difficult the establishment of native grasses.

Gaps in many areas of NW Patagonia's grasslands are invaded by *Rumex acetosella* (sheep sorrel, Polygonaceae; hereafter *Rumex*) (Franzese and Ghermandi, 2012b), a cosmopolitan ruderal herb that has successfully invaded the region. This species has great colonization ability on disturbed free-vegetation areas (Ghermandi et al., 2004; Gobbi et al., 1995), and might interfere with secondary succession processes and gap colonization dynamics of native species. Furthermore, under certain conditions *Rumex* has the ability to competitively exclude native tussock grasses. Fan (1996) showed that *Festuca novae-zelandiae*, an unpalatable grass from New Zealand, was displaced by *Rumex* on fertile soils. Also, it has been reported that heavy grazing can allow *Rumex* to be competitive with forage grasses (Leedje et al., 1981). Although *Rumex* occurs worldwide (Stopps et al., 2011) and that it has been identified as an invasive species in many countries (with high detrimental economic impacts in some of them; Stopps et al., 2011), little information on the competitive effects of this species is available. In particular for Patagonian grasslands, little is known about the competitive ability of native grasses in presence of *Rumex* during early growth or whether native grasses that differ in the degree of stress tolerance and palatability compete different with *Rumex*.

A greenhouse experiment was conducted to study the effect of *Rumex* competition under different summer precipitation regimes on early growth of the two dominant tussock grasses. We compared the relative competitive ability of the exotic herb in relation to each native species, as well as growth responses of all three species growing without competition in two contrasting watering conditions. We hypothesized that *Rumex* outcompetes native grasses in an early developmental stage (inter-specific even-size interactions), and that *Pappostipa* (the unpalatable grass species with greater tolerance to water stress) has lower competitive ability than *Festuca*.

2. Methods

2.1. Study area and plant species

Seeds were collected from a semiarid grassland in NW Patagonia, Argentina (41°03'19"S–71°01'50"W). Mean annual precipitation is 580 mm (60% falls in autumn and winter) and mean annual temperature is 8.6 °C (San Ramón ranch meteorological station). Gap areas cover approximately 40% and are colonized by native and exotic herb species (detailed description in Franzese and Ghermandi, 2012a). Gaps are dominated by *Rumex*, an unpalatable for livestock species which is native to Europe and widely distributed in temperate environments of the world, commonly in open and/or disturbed habitats (Correa, 1984). This herb reproduces clonally (ramets produced from root and rhizome buds) and sexually, and forms persistent seed banks. *Pappostipa* and *Festuca* reproduce from seeds and form transient seed banks. *Rumex* is among the most abundant species in the soil seed bank and has greater relative importance than perennial grasses which are rare or absent from the seed bank (Ghermandi, 1992; Gonzalez and Ghermandi, 2008). All three species germinate in the spring

(September–October) and face the period of highest water stress in summer (particularly January–February months).

2.2. Experimental design

Seeds from the three species were collected randomly from several individuals in February–March 2007 and stored in paper bags at room temperature until the experiments were performed. We selected the viable seeds using the pressure method (Zuluaga et al., 2004) for *Festuca* and *Rumex* seeds, and the flotation method for *Pappostipa* seeds. In October 2007, we sowed seeds from each species in trays (one seed per 150 cm³ tray) with grassland soil that was previously sterilized (2 days at 100 °C) to kill the soil seed bank. Trays were watered to field capacity until February 2008, when we performed the competition treatments. We let seedlings grow for four months before treatments set up because we wanted to simulate competition at the age where seedlings face the greatest water stress in field. For competition treatments, we used a total of 130 seedlings per species. Twenty six seedlings of each species were transplanted into individual pots (13 × 15 × 15 cm³) filled with grassland soil, which were watered to field capacity for a week (control: without competition treatment). The remaining 104 seedlings of each species were assigned to inter-specific competition treatments. We transplanted four seedlings per pot, combining two species (i.e. 2 plants per species): *Rumex* + *Pappostipa*, *Rumex* + *Festuca*, and *Festuca* + *Pappostipa*. Competition among grasses was quantified to relativize the effect of *Rumex* competition on each grass species (Vilà and Weiner, 2004). Half of the pots per treatment (with or without competition) were watered simulating a wet summer ($n = 13$), while the remaining pots were watered simulating a dry summer ($n = 13$ per treatment). We used the monthly summer precipitation values that were higher than the mean historical precipitation (1959–2007, San Ramon meteorological station) to calculate the average water amount to simulate a wet condition (February: 36 mm, and March: 40 mm). We also used the monthly summer precipitation values that were lower than the mean historical precipitation (excluding those <4 mm) to calculate the average water amount to simulate a dry condition (February: 10 mm, and March: 15 mm). The water amount per pot was calculated by multiplying the monthly rainfall by the pot area, and dividing this result by watering days per month (12 days, three times per week). At the end of the experiment, we measured height (cm; only in grasses), root length (cm; only in grasses), and weighed the dry biomass (g; 60 °C for 24 h) from all seedlings. Since clonality is an important trait for *Rumex* ecology, we also counted the underground buds in this species.

2.3. Data analysis

To assess how competition and watering treatments affected early growth of dominant tussock grasses, we performed two-way ANOVAs with competition (three levels: control, competition with *Rumex*, and competition with the co-dominant grass) and watering condition (two levels: dry and wet) as factors. The analyzed variables were height, root length, and above-ground and root biomass. Data were log-transformed prior to the analysis whenever they did not meet the assumptions for the parametric tests (in *Pappostipa*: height, above-ground biomass, and root length; in *Festuca*: height, above-ground biomass, and root biomass). We also performed a two-way ANOVA to analyze the effect of treatments on total underground *Rumex* buds. We carried out orthogonal contrasts to assess how competition affected growth in each watering condition. Also, for each species, we compared: a) total biomass between watering conditions (control treatment; independent samples) using *t* tests or Mann–Whitney tests (non-parametric data), and b)

above-ground biomass against root biomass within each watering condition (control treatment; dependent samples) using *t* tests for dependent samples or Wilcoxon tests (non-parametric data). The significance level was $\alpha = 0.05$.

3. Results

3.1. Effect of *Rumex* and *Festuca* competition on *Pappostipa* growth

Seedling height was influenced by competition and watering, although these factors did not interact (C: $F_{2,72} = 12.9, P < 0.001$; W: $F_{1,72} = 12.6, P < 0.001$; C x W: $F_{2,72} = 1.3, P > 0.05$; Appendix 1a). In both watering conditions, the competitors decreased height in similar proportions (orthogonal contrasts: each $P > 0.05$; Fig. 1a). Above-ground and root biomass production depended on watering and competition (above-ground biomass: C x W: $F_{2,72} = 7.05, P < 0.01$; root biomass: C x W: $F_{2,72} = 3.5, P < 0.05$; Appendix 1a). In dry conditions, *Pappostipa* above-ground and root biomass were more affected by *Festuca* than by *Rumex* (orthogonal contrasts: each $P < 0.05$). Compared with control, *Festuca* presence reduced above-ground biomass by 48% (Fig. 1c) and root biomass by 31% (Fig. 1e). In wet conditions, competitors affected above-ground biomass similarly but did not affect root biomass (orthogonal contrasts: each $P > 0.05$; Fig. 1e). Root length was not affected by competition treatments (Fig. 1g; Appendix 1a). In short, the impact of *Rumex* on early growth of *Pappostipa* was similar to the impact of *Festuca* on *Pappostipa* growth. In some cases (above-ground and root biomass in dry conditions), *Rumex* had a smaller impact than *Festuca* on *Pappostipa* growth.

3.2. Effect of *Rumex* and *Pappostipa* competition on *Festuca* growth

Seedling height was influenced by competition and watering, with no interaction between these factors (C: $F_{2,72} = 9.0, P < 0.001$; W: $F_{1,72} = 45.4, P < 0.001$; C x W: $F_{2,72} = 1.9, P > 0.05$; Appendix 1b). In dry conditions, the competitors decreased height in similar proportions (orthogonal contrast: $P > 0.05$), but in wet conditions *Rumex* presence reduced *Festuca* height by 21%, a proportion significantly higher than the reduction caused by *Pappostipa* presence (3.5%) (orthogonal contrast: $P < 0.01$; Fig. 1b). Above-ground biomass decreased in presence of both competitor species, but *Rumex* produced a major impact on this variable in wet conditions (56% and 46% less above-ground biomass with *Rumex* and *Pappostipa*, respectively) (orthogonal contrast: $P < 0.01$; Fig. 1d), that was compensated for higher root biomass production (orthogonal contrast: $P = 0.05$; Fig. 1f). In dry conditions, the presence of *Pappostipa* caused a 45% of reduction in root biomass, which was significantly greater than the reduction produced by *Rumex* (16.5%) (orthogonal contrast: $P < 0.01$; Fig. 1f). The competitors' presence diminished root length in dry conditions, but slightly increased root length in wet conditions (orthogonal contrasts: each $P < 0.01$; Fig. 1h; Appendix 1b). To summarize, *Rumex* competition decreased height and above-ground biomass of *Festuca* more than competition from *Pappostipa* (only in wet conditions), but there was a compensation effect observed mainly in root biomass. Instead, *Pappostipa* had a greater negative effect on *Festuca* root biomass than *Rumex* (only in dry conditions).

3.3. Effect of treatments on *Rumex* underground buds

Rumex produced buds in all competition-watering treatments (mean bud range: 5–11; Fig. 2). Total bud production was not affected by watering conditions, but it was affected by competition (Fig. 2; Appendix 1c).

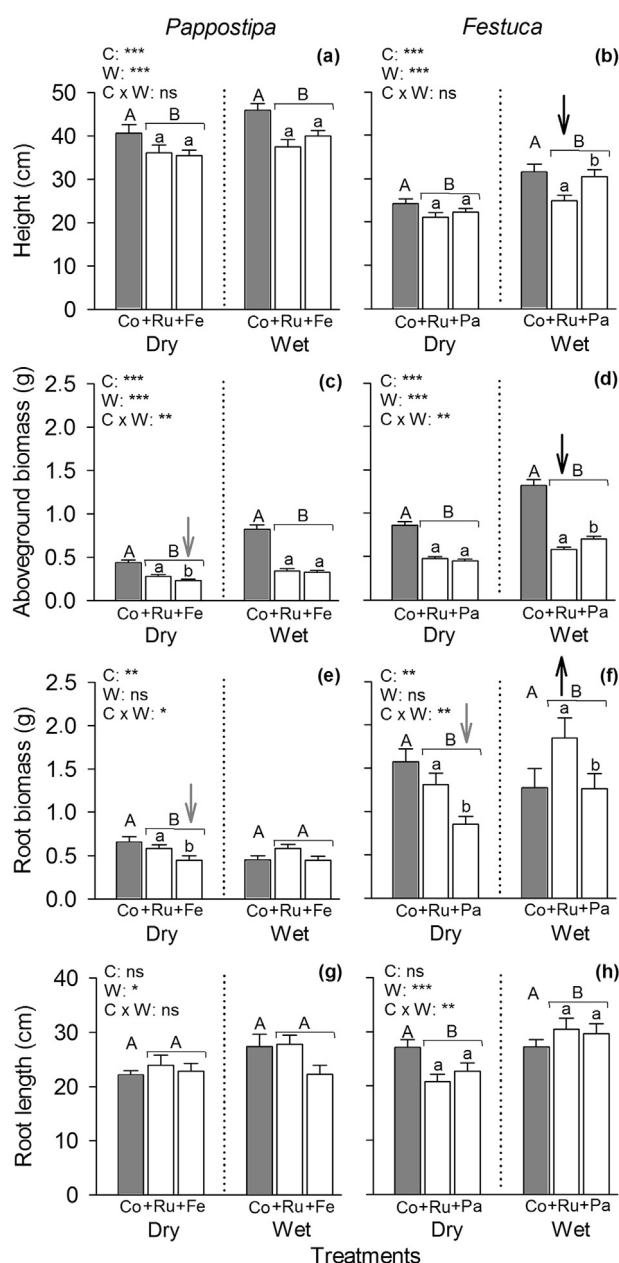


Fig. 1. Early growth of *Pappostipa* (left column) and *Festuca* (right column) in different competition (C) and watering (W) treatments. Co: control (without competition, gray bars); +Ru: competition with *Rumex*; +Fe: competition with *Festuca*; +Pa: competition with *Pappostipa*. Black arrows pointing down indicate a greater competitive effect of *Rumex* in comparison to *Pappostipa* on *Festuca* growth, while gray arrows indicate a greater competitive effect of native grasses in comparison to *Rumex*. The black arrow pointing up indicates a greater growth of *Festuca* in presence of *Rumex*. Letters indicate statistical comparisons between competition treatments within each watering condition: capital letters show comparisons between control and the other two competition levels, and small letters show comparisons between the levels within competition (i.e. +Ru vs. +Fe or +Ru vs. +Pa).

3.4. Early plant growth responses in two contrasting watering conditions

In dry conditions, both grass species produced greater root biomass than above-ground biomass (Fig. 3a, b). However, in wet conditions there were differences in the resource allocation among species: while *Pappostipa* produced twice above-ground biomass than root biomass (Fig. 3a), *Festuca* produced similar amounts of

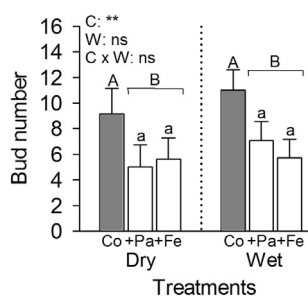


Fig. 2. Mean *Rumex* bud number in different competition (C) and watering (W) treatments. Co: control (without competition, gray bars); +Pa: competition with *Pappostipa*; +Fe: competition with *Festuca*. Letters indicate statistical comparisons between competition treatments within each watering condition: capital letters show comparisons between control and the other two competition levels, and small letters show comparisons between levels within competition (i.e. + Pa vs.+Fe).

above-ground and root biomass (Fig. 3b). On the other hand, *Rumex* assigned a greater amount of resources to root than above-ground biomass, and produced twice the biomass in wet conditions compared to dry conditions (Fig. 3c).

4. Discussion

Our results suggest that *Rumex* seedlings can interfere on early growth of the dominant tussock grass species from NW Patagonia, but its relative impact (i. e. compared to the effect produced by other common native species) would not be greater to that of any co-dominant grasses. The native grass species studies here did not show the expected trade-off between stress tolerance and competitive ability (Grime, 1979; Liancourt et al., 2005) when considering inter-specific even-size interactions established in an early developmental stage. It is possible that seedlings may not have developed yet the distinctive characters that distinguish adults in terms of palatability and tolerance to water stress. An experimental study showed that the relative palatability to herbivores of seedlings and adults of the same species may differ widely (Fenner et al., 1999). Since palatability traits are closely related to a number of ecophysiological characteristics that determine drought tolerance (Moreno et al., 2010; Woodman and Fernandes, 1991), it is possible that the discrepancy in palatability between seedling and adult stages could be also reflect differences in drought tolerance strategy. Thereby, young individuals of both grass species would acquire adult's distinctive features with time, in a process

shaped in part by the characteristics of the prevailing environmental gradient.

Although seedlings of grass species were not affected differentially by *Rumex* competition, they show a differential fitness (reflected in biomass allocation) when growing without competition and with abundant water, the most favorable simulated environmental condition. In this case, while *Festuca* produced similar proportions of above-ground and root biomass, *Pappostipa* produced twice as much above-ground biomass as root biomass. These results may reveal a better fit of the unpalatable grass to the prevalent environmental conditions, because it allocates resources more effectively. However, *Festuca* had enough plasticity to reallocate resources to root growth in the presence of *Rumex* in a simulated wet summer. Fernández et al. (2004) found that *Festuca* changed the biomass allocation pattern when grown under shade conditions, increasing the proportion of leaves relative to the roots in comparison to the open grassland. In our experiment, most of the leaves produced by *Rumex* were prostrate and did not shade *Festuca* canopy. Therefore we suggest that above-ground competition was negligible, and that the increase in *Festuca* root biomass was a response of increased underground competition under wet conditions. Some authors have failed to find a trade-off between aboveground cover and root biomass in grassland species (Rodríguez et al., 2007) or a clear pattern of plasticity in biomass allocation as a response to different competition treatments (Aerts et al., 1991). Since biomass allocation pattern is regulated by genetic and local environmental controls (Robinson et al., 2010), competitive ability is a plastic trait greatly influenced by the surrounding biophysical context.

In the experimental conditions that simulated a dry summer, there was a strong underground competition among grass species, but there was no evidence of *Rumex* competition with neither *Festuca* nor *Pappostipa*. On one hand, the intense competition among grasses could be due to similar strategies of resources acquisition since both species belong to the same functional group (Golluscio et al., 2005). These results are similar to others obtained in Patagonia, where significant competition for water was reported among native grasses (Defossé et al., 1997; Graff et al., 2007), and support the fact that water is the main limiting resource for plant establishment in the Patagonian steppes (Bertiller et al., 1996; Defossé et al., 1997). On the other hand, *Rumex* growth greatly decreases under water stress (Houssard et al., 1992; Zimmerman and Lechowics, 1982). Unlike the grasses, whose biomass production did not vary between watering conditions when grown without competition, *Rumex* doubled its biomass when grown with abundant water. A rapid response to optimal conditions could be related to a low tolerance to drought (Bunce, 1981 in Houssard et al., 1992), which is expected in a species that is also common in floodplain and riparian habitats (U.S. Forest Service, 2011). In vegetation records from NW Patagonia, *Rumex* was absent or rare towards the east in sites where annual rainfall is lower than 250 mm (Speziale K., Personal communication). In addition, the fast growth of *Rumex* in favorable conditions would allow it to capture of water and nutrients quickly, reducing availability of these resources for slow-growing grass species (Fan, 1996).

Rumex produces an extensive belowground system of buds that constitute a source for potential shoot growth (Klimešová and Klimeš, 2006). This species spreads underground (supported by photosynthate transported from illuminated parts of the canopy; Harris, 1972 in Fan, 1996), and colonizes gaps vegetatively with the emergence of new shoots (Fan, 1996; Personal observation). The importance of underground buds was reflected in our experiments since their production was initiated in the very early development (three month-old plants, Personal observation) and was maintained even under unfavorable conditions such as water stress or inter-specific competition. The energy investment in the

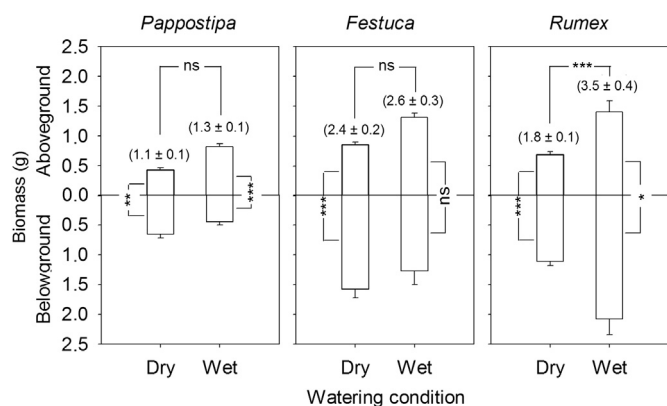


Fig. 3. Mean aboveground and belowground biomass (g) of *Pappostipa*, *Festuca* and *Rumex* in two watering conditions (data from control treatment for each species). Values between parentheses show each species' total biomass. Asterisks between lines show statistically significant differences between the connected bars. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, ns: non-significant differences.

production of reserve organs, despite the prevalent environmental conditions, could play an important ecological role for *Rumex*, probably insuring its persistence and spread in grassland gaps once the plants are established.

Overall, our results indicate that *Rumex* seedlings have a negative impact on dominant grass seedlings, but it is not greater than that produced by native grasses. The studied grasses did not differ in sensitivity to early competition by *Rumex* or water stress. However, it is important to keep in mind that competitive balance among species can change with time, and be considerably altered by grazing. The low competitive ability of *Rumex* under water stress could indicate that its invasive potential from a seedling stage would be controlled by the aridity of the environment. Our study also showed that there can be an early contribution of buds from *Rumex* seedlings to the soil bud bank, a key eco-biologic trait of this invasive species. Therefore, the estimation of the bud bank abundance and the study of how vegetative regeneration may be interfering with recruitment of dominant grasses should be considerate in future research.

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Appendix 1. Analysis of variance results for growth variables in response to competition, watering and their interaction in *Pappostipa* (a), *Festuca* (b), and *Rumex* (c). † Variable log-transformed.

(a) <i>Pappostipa</i> source of variation	df	Height†		Above-ground biomass†		Root biomass		Root length†	
		F	P	F	P	F	P	F	P
Competition	2	12.9	<0.001	97.9	<0.001	5.1	<0.01	2.9	>0.05
Watering	1	12.5	<0.001	69.6	<0.001	3.8	>0.05	5.4	<0.05
Competition × Watering	2	1.3	>0.05	7.0	<0.01	3.5	<0.05	2.1	>0.05
Error	72								

(b) <i>Festuca</i> source of variation	df	Height†		Above-ground biomass†		Root biomass†		Root length	
		F	P	F	P	F	P	F	P
Competition	2	9.0	<0.001	172.8	<0.001	7.1	<0.01	0.6	>0.05
Watering	1	45.4	<0.001	108.3	<0.001	1.3	>0.05	25.1	<0.001
Competition × Watering	2	1.9	>0.05	5.6	<0.01	5.9	<0.01	6.5	<0.01
Error	72								

(c) <i>Rumex</i> source of variation	Bud number		
	df	F	P
Competition	2	6.1	<0.01
Watering	1	1.4	>0.05
Competition × Watering	2	0.2	>0.05
Error	72		

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